

Hidden diversity of *Freyastera* (Asteroidea, Brisingida, Freyellidae) at great depth: Description of new species and remarks on species boundaries

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Abstract

Freyastera represents the most derived form in the deep-sea starfish order Brisingida, known only at below 2500 m to over 6000 m depth, adapting to the great depth by small body size, reduced number of arms, and simplified body form. Long being remote and rarely investigated, newly collected specimens from the last decade revealed high species diversity of the genus. In this study, a new species, *Freyastera jiaolongi* **sp. nov.**, is described from the southern part of the Kyushu-Palau Ridge. *Freyastera giardi* **comb. nov.** and *Freyastera loricata* **comb. nov.**, formerly belonging to genus *Freyella*, are reassigned to *Freyastera*. The genus is hence revised to include ten species. Key characters of nine *Freyastera* species as well as *Freyella benthophila* (formerly *Freyastera benthophila*) are described and discussed based on an examination of type specimens and new specimens, and a key to *Freyastera* species is provided, aiding in the future identification of *Freyastera*. Phylogenetic analysis using four DNA barcoding genes retrieves a monophyletic *Freyastera*, providing solid support for interspecific phylogeny except at three nodes. Species delimitation analysis results in 11 species units within *Freyastera*, including seven unnamed species pending description. A high diversity of *Freyastera* revealed in the present study suggests a successful adaptation and radiation of the genus at great depth.

Key Words

Deep-sea, phylogeny, species delimitation, taxonomy

Introduction

Genus *Freyastera* Downey, 1986, belonging to the family Freyellidae, order Brisingida, is a group of starfish living exclusively in the deep ocean from lower bathyal to hadal depth. They were known at 2645 m the shallowest (NOAA Ocean Exploration 2024), to 6415 m the deepest (Zhang et al. 2019), being most diverse in the abyssal zone (4000 m to 6000 m) (Galkin and Korovchinsky 1984; Zhang et al. 2019). In contrast to other Brisingida species which possess numerous arms (up to 20), *Freyastera* displays only six long and slender arms with

a small disk. A simplification of starfish morphology in relation to the great depth was considered as an adaptive strategy (Mironov et al. 2016) and may be owing to a paeomorph development, which was also found in several other Brisingida species (Zhang et al. 2024). *Freyastera* is thus an ideal target to investigate the diversification and adaptation of fauna at great depth.

Freyastera was established by Downey in 1986, accommodating four species that were previously classified as *Freyella* Perrier, 1885. McKnight (2006), Zhang et al. (2019), and Zhang et al. (2024) further added three new species and revised the genus, resulting in a total of

seven nominal species of *Freyastera* (Mah 2025). It was once thought that all six-armed freyellids are close to and may belong to *Freyastera* (Mah 1998; Zhang et al. 2019). However, the latest study (Zhang et al. 2024) showed that *Freyastera benthophila* (Sladen, 1889), although having six arms and traditionally classified as *Freyastera* (Downey 1986), was genetically distinct from other *Freyastera* species. Phylogenetic analyses placed it in a clade formed by *Freyella* species, which all have more than six arms (Zhang et al. 2024). This indicated that the possession of six arms is not an autapomorphy of the *Freyastera* clade, and the number of arms should not be considered as the sole character to differentiate *Freyastera* and *Freyella*. *Freyastera benthophila* was reassigned as *Freyella* based on this result (Zhang et al. 2024). This finding has challenged the previous understanding of the boundaries of genera, and the taxonomic position of all the six-armed freyellids needs to be re-evaluated. Furthermore, the same research has provided genetic data of a large number of undescribed species that almost doubled the known diversity of *Freyastera*, but owing to the scope of that study, detailed taxonomic description and discussion of *Freyastera* species were not provided (Zhang et al. 2024).

In the present study, we present the systematic accounts on *Freyastera* and six-armed *Freyella* based on the dataset of Zhang et al. (2024) and additional specimens collected from the latest cruises. A new species, *Freyastera jiaolongi* sp. nov., is described, and two new species combinations are proposed. A diagnostic key and a phylogenetic tree for *Freyastera* species are provided, and boundaries among species using genetic and morphological evidence are investigated, aiding in the future identification of *Freyastera*.

Materials and methods

Sample collection and preservation

A total of 43 *Freyastera* specimens and 26 *Freyella benthophila* specimens were examined in the present study, of which 64 specimens were included in the dataset of Zhang et al. (2024). A majority of the specimens studied were loaned from the following institutes: German Centre for Marine Biodiversity Research, Senckenberg am Meer (DZMB), Institute of Deep-sea Science and Engineering, Chinese Academy of Sciences (IDSSE), P. P. Shirshov Institute of Oceanology, Russian Academy of Sciences (IORAS), Muséum national d'Histoire naturelle (MNHN), Musée Océanographique de Monaco (MOM), Natural History Museum (NHMUK), National Oceanography Centre (NOC), and Université Libre de Bruxelles (ULB). Five additional specimens were collected during Chinese cruises DY68 in 2021, DY80I in 2023, and DY86II in 2024 by HOV *Jiaolong* from the Northwest Pacific. These specimens were photographed on board using a digital camera (Canon EOS 7D), then fixed and preserved in pure ethanol. Collection information of all specimens studied is listed in Suppl. material 1.

Morphological examinations

Specimens were examined under a stereoscope (Zeiss Axio Zoom.V16) or a microscope. The following measurements were obtained for each specimen: *r* (radius of disk), *R* (distance between disc center and arm tip), height of disk (*Hd*), width of arm base (*Wb*), largest width of arm in genital area (*Wg*), and length of genital area (*Lg*). Morphological characters were examined and photographed, sometimes under dry conditions for better observation. Key characters for species delimitation mainly include the armature and spination of the abactinal disk and arm, the form and arrangement of spines on the oral plate and adambulacral plate, the size and arrangement of pedicellariae, the arrangement of inferomarginals and lateral spines, and the form of gonads. Description of species and characters follows Sladen (1889), Perrier (1885, 1894), Koehler (1907, 1908), A.H. Clark (1939), Madsen (1956), Korovchinsky and Galkin (1984), Downey (1986), McKnight (2006), Zhang et al. (2019), and Zhang et al. (2024).

Molecular phylogenetic analysis

DNA extraction, gene amplification, and sequencing procedures were as described in Zhang et al. (2024). Barcoding regions of the mitochondrial cytochrome *c* oxidase subunit I (COI), the mitochondrial 16S ribosomal RNA (16S), the mitochondrial 12S ribosomal RNA (12S), and the nuclear 28S ribosomal RNA (28S) were obtained for phylogenetic analyses and molecular species delimitation. Genetic data from *Freyella attenuata*, *Freyella benthophila*, and *Freyella echinata* published in Zhang et al. 2024, were used as an outgroup. Additional sequences obtained in the present study were submitted to the GenBank repository (see Suppl. material 1 for GenBank accession numbers). Sequences were aligned using the MUSCLE algorithm (Edgar 2004) implemented in Geneious Prime (Kearse et al. 2012). Alignment of 16S was cured in Gblocks 0.91b (Castresana 2000) under less stringent selection options. DAMBE 7 (Xia 2018) was used to test for substitution saturation in the protein-coding gene COI, and saturation was not detected.

Four gene alignments were concatenated, and partitions were set for each gene fragment and each codon position of COI. Phylogenetic trees were constructed using maximum likelihood (ML) and Bayesian inference (BI) methods. ModelFinder (Kalyaanamoorthy et al. 2017), implemented in IQ-TREE v2.0 (Minh et al. 2020), was used for the best model estimation. The following models were selected and used in maximum likelihood analysis: COI (1st codon site: TNe+I; 2nd codon site: F81+F+I; 3rd codon site: HKY+F+G4), 16S (HKY+F+I+G4), 12S (TIM2+F+I+G4), and 28S (HKY+F+I). Maximum likelihood analysis with 100,000 ultrafast bootstrap (Hoang et al. 2018) replicates was run in the IQ-TREE local server. Bayesian reconstruction was conducted using MrBayes v3.2.7 (Huelsenbeck and Ronquist 2001), with four parallel runs of 10,000,000 generations executed with four chains, sampling at every

1,000 generations. The first 25% of trees were discarded as burn-in. TRACER v. 1.7 (Rambaut et al. 2018) was used to check for run convergence. The tree topologies were observed and edited in Figtree v1.4.3.

Species delimitation and genetic distance

Species were delimited primarily based on morphological characters, and the molecular species delimitation tool Assemble Species by Automatic Partitioning (ASAP; Puillandre et al. 2021) was used as a validation method. ASAP uses pairwise genetic distances and a scoring system to define species groups. The Jukes-Cantor (JC69), Kimura (K80), and Simple Distance (p-distances) substitution models were selected on the ASAP web server (<https://bioinfo.mnhn.fr/abi/public/asap/>) for COI and 16S alignments. COI genetic distances (K2P, Kimura 1980) were calculated in MEGA 11 (Tamura et al. 2021).

Spatial distribution analyses

To evaluate the global and bathymetric distribution of *Freyastera* and closely related species, the coordinates and depth information of type specimens of *Freyastera* and six-armed *Freyella* species were compiled. Together with the information of the non-type specimens examined in the present study, a total of 77 records were used in spatial distribution analyses. The global distribution map was generated using QGIS 3.28.0-Firenze (QGIS Development Team 2024). A bathymetric distribution map was drawn using the R package ggplot2 (Wickham 2016) in RStudio 2023.09.1 (RStudio Team 2024).

Nomenclatural acts

The new names contained in this article are available under the International Code of Zoological Nomenclature. This work and the nomenclatural acts it contains have been registered in ZooBank. Zoobank Life Science Identifier (LSID) for this publication is: urn:lsid:zoobank.org:pub:4611CD60-658B-42C4-B23C-2DA9185A85E3. The LSID registration and any associated information can be viewed in a web browser by adding the LSID to the prefix <http://zoobank.org/>.

Results

Systematics

Order Brisingida Fisher, 1928

Family Freyellidae Downey, 1986

Genus *Freyastera* Downey, 1986

Type species. *Freyella sexradiata* Perrier, 1885.

Diagnosis. Arms six. Papulae absent. One pair of gonads on each arm. Disk very small, arms extremely long and slender. The first pair of inferomarginal plates appears later on arm, not in contact with the odontophore. Inferomarginal plates and lateral spines generally correspond to every adambulacral plate beyond genital area. Abactinal arm in genital region covered with pavement of spinate plates. Adambulacral plates elongated.

Remarks. *Freyastera* and *Freyella* were redefined by Zhang et al. (2024), with the number of arms and the arrangement of inferomarginal plates as key diagnostic characters. The genus *Freyastera* currently contains seven species (Mah 2025): *Freyastera basketa* Zhang et al., 2019; *Freyastera delicata* Zhang et al., 2019; *Freyastera digitata* McKnight, 2006; *Freyastera mexicana* (A.H. Clark 1939); *Freyastera mortenseni* (Madsen 1956); *Freyastera sexradiata* (Perrier 1885); and *Freyastera tuberculata* (Sladen 1889). A new species, *Freyastera ji-aolongi* sp. nov., is described in the present study. Two species previously belonged to *Freyella*, *F. giardi* Koe-hler, 1907, and *F. loricata* Korovchinsky & Galkin, 1984, are reassigned here to *Freyastera* as new species combinations. The genus is hence composed of 10 species in total. Furthermore, seven unnamed species are included in the molecular analyses: *Freyastera* sp. 2, *Freyastera* sp. 3, *Freyastera* sp. 5, *Freyastera* sp. 6, *Freyastera* sp. 7, *Freyastera* sp. Yap, and *Freyastera* cf. *tuberculata*. Among them, precise identification of *Freyastera* sp. 2, *Freyastera* sp. 7, and *Freyastera* cf. *tuberculata* was not feasible, as they were morphologically similar to *Freyastera tuberculata*, *Freyastera giardi* comb. nov., and *Freyastera loricata* comb. nov. (see *Freyastera tuberculata* species complex). *Freyastera* sp. Yap (RSIOAST0041) was reported based on one broken arm (Zhang et al. 2019), whereas specimens of *Freyastera* sp. 3 (RSIOAST0057), *Freyastera* sp. 5 (RSIOAST0107, RSIOAST0116, RSIOAST0138) (Fig. 14F–G), and *Freyastera* sp. 6 (RSIOAST0124, RSIOAST0125) (Fig. 14H, I) were severely damaged during collection, with only arm fragments available, or kept frozen after collection, which hinders proper morphological identification and description. However, genetic information from these specimens showed high diversity, and species delimitation tools set them as seven species units, distinguishable from other known species with genetic data available. They were therefore included in the present study to discuss the phylogeny and diversity of *Freyastera*. Proper definition and description of these species units need to be done with more specimens in good condition in the future.

The following systematic accounts include a key, diagnoses, illustrations, and remarks on each known *Freyastera* species or species complex based on specimens or photos examined, except one species, *Freyastera digitata* McKnight, 2006. *F. digitata* was described to have an inferomarginal plate corresponding to every 2–3 adambulacral plates (McKnight 2006), but the holotype was broken with only 22 mm of arm left, thus the arrangement of inferomarginal plates beyond the genital area is largely unknown. This species greatly resembles

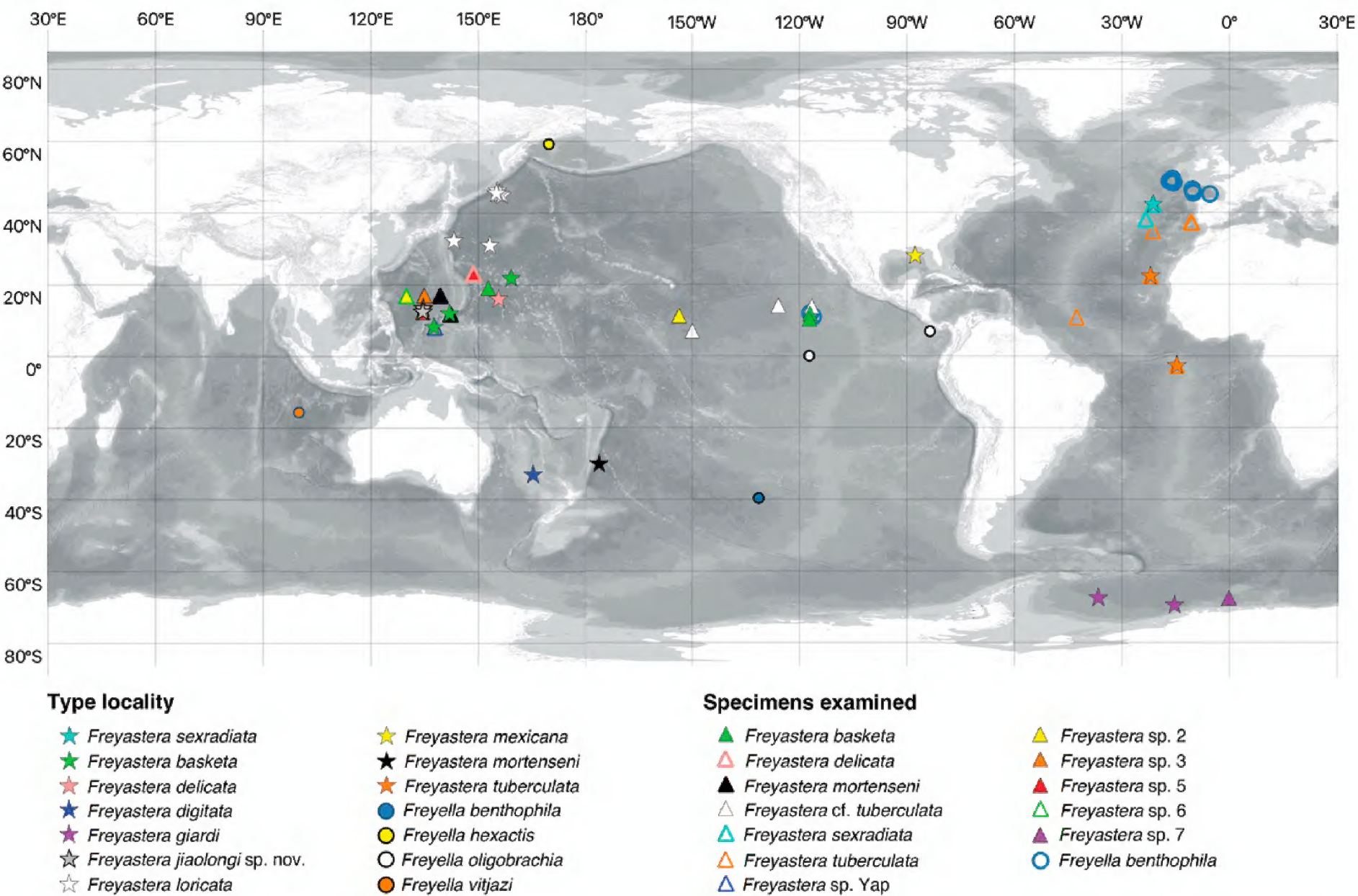


Figure 1. Distribution of *Freyastera* and six-armed *Freyella* specimens examined in the present study and type localities of each species.

Freyella benthophila in the absence of a furrow spine and abactinal plates with several short spinelets. The taxonomic position of *F. digitata* needs to be re-evaluated with further examination of the holotype and other complete specimens. It is thus not included in the diagnostic key of the genus for the time being.

Key to *Freyastera* species

- 1 large pedicellariae present on abactinal surface of disk and arm genital area, as well as on oral spines..... 2
- large pedicellariae absent..... 3
- 2 abactinal plate on arm each with one spine *F. basketa*
- abactinal plate on arm each with multiple spines..... *F. mortenseni*
- 3 abactinal plate on arm each with multiple spines, not covered by membranous sheath..... 4
- abactinal plate on arm each with one spine, covered by membranous sheath 5
- 4 adambulacral spines 4–5, forming a diagonal row; oral spines 9–12 *F. mexicana*
- adambulacral spines 2–3; oral spines 4 *F. delicata*
- 5 furrow spine absent..... *F. giardi*/*F. loricata*/*F. tuberculata* (*F. tuberculata* species complex)
- furrow spine present 6
- 6 abactinal disk with short spinelets, each surrounded by 2–6 small pedicellariae..... *F. jiaolongi* sp. nov.
- abactinal disk with fairly elongate spines, devoid of pedicellariae..... *F. sexradiata*

***Freyastera jiaolongi* sp. nov.**
<https://zoobank.org/316a8a05-1665-4602-aa2f-566281c4e451>
Figs 2–4, 14A–C

Freyastera sp. 4: Zhang et al. 2024.

Material examined. Holotype. RSIOAST0117 (Figs 2, 3), Kyushu-Palau Ridge; 12.330671°N, 134.472114°E, 3523 m; 16 Nov. 2021; cruise DY68, dive JL199.

Paratype 1. RSIOAST0112 (Fig. 3A, D), Kyushu-Palau Ridge; 13.309640°N, 134.591983°E, 3641 m; 13 Nov. 2021; cruise DY68, dive JL197. **Paratype 2.** RSIOAST0113 (Fig. 3B, C, E, F), Kyushu-Palau Ridge; 13.310851°N, 134.589032°E, 3541 m; 13 Nov. 2021; cruise DY68, dive JL197. All type specimens were deposited at the Repository of Second Institute of Oceanography, Ministry of Natural Resources, China (SIOMNR) (Suppl. material 1).

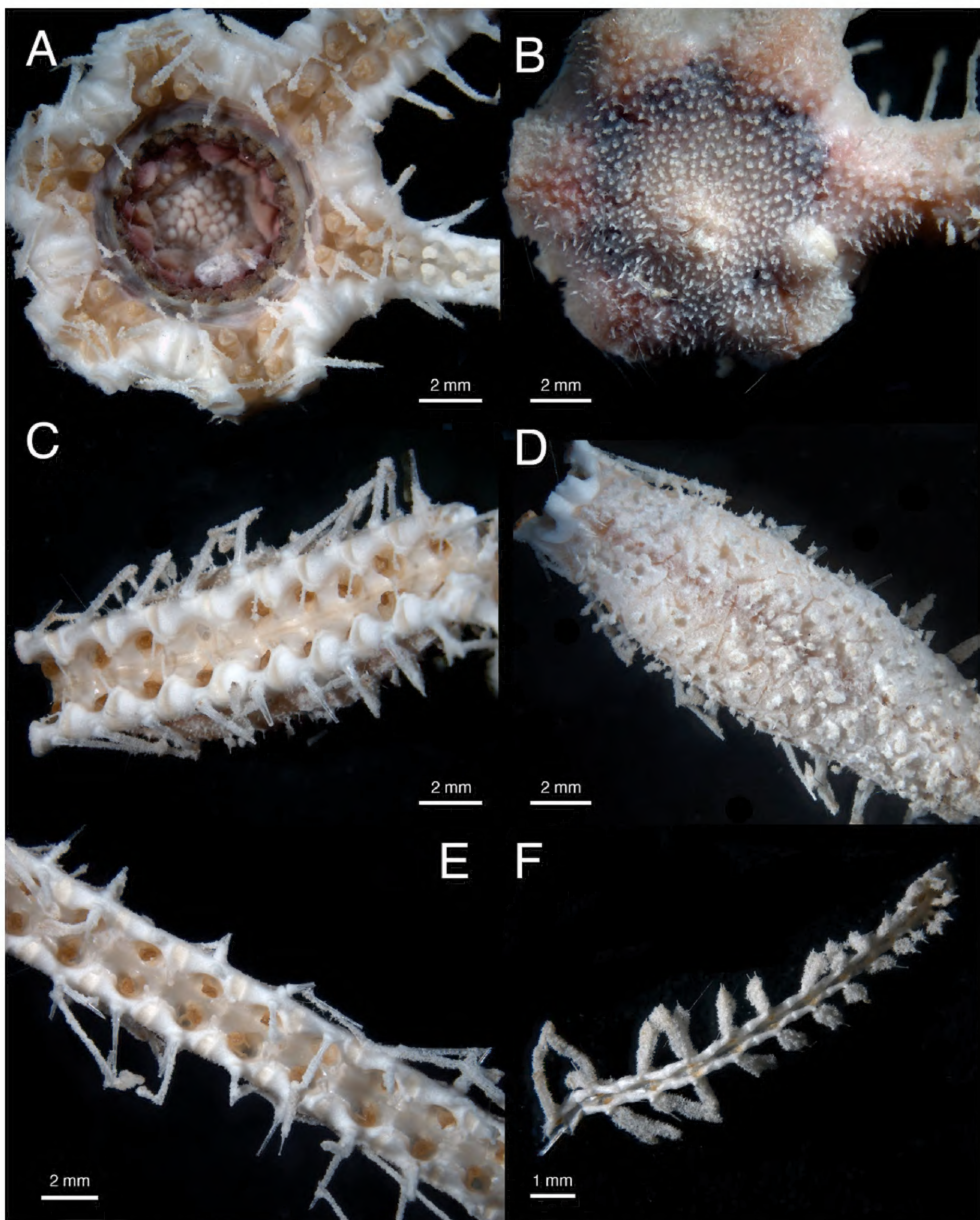


Figure 2. *Freyastera jiaolongi* sp. nov. holotype RSIOAST0117. **A.** Actinal view of disk; **B.** Abactinal view of disk; **C.** Actinal view of arm in genital area; **D.** Abactinal view of arm in genital area; **E.** Actinal view of middle part of arm; **F.** Actinal view of distal part of arm.

Diagnosis. Arms six. Abactinal disk with short hirsute spinelets, about 0.2 mm in length, surrounded by small pedicellariae. Abactinal arm plates each bears one spine, covered with a membranous sheath loaded with small pedicellariae. Pedicellariae on abactinal disk and arm less than 0.1 mm in length. Pedicellariae cluster in pads or

transverse bands on abactinal arm beyond genital area. Each adambulacral plate with 1–3 aboral furrow spines and one subambulacral spine. Lateral spines long, corresponding to each adambulacral plate beyond genital area. Oral plate with 1–2 actinostomal spines, one sub-oral spine, and one aboral spine along the furrow margin.

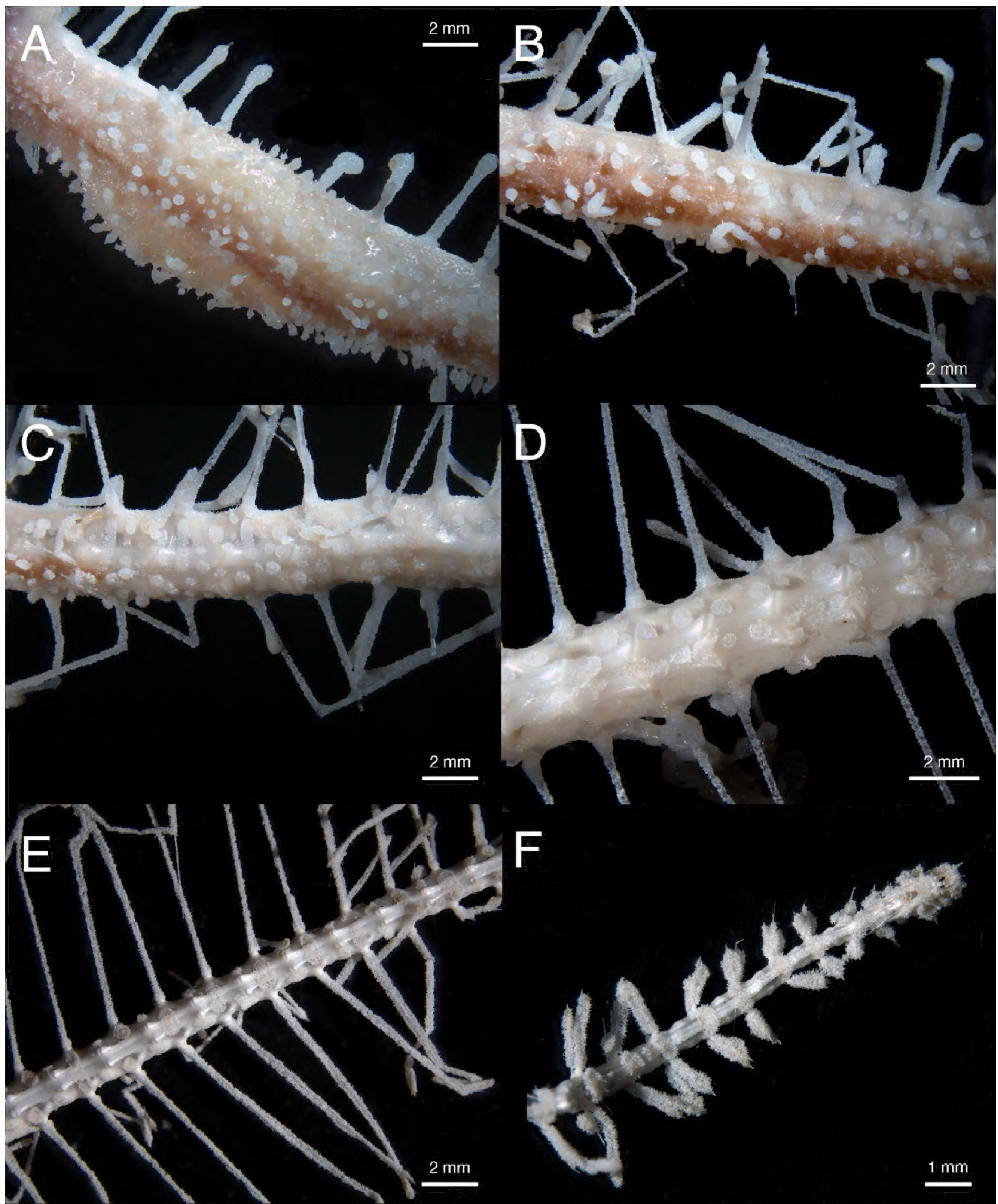


Figure 3. *Freyastera jiaolongi* sp. nov. holotype RSIOAST0117. **A–D.** Abactinal view of arm, from basal part to beyond genital area; **E.** Abactinal view of middle part of arm; **F.** Abactinal view of distal part of arm.

Description. Holotype: a complete specimen, with one arm regenerating. $r = 5.5$ mm, R about 220 mm. Height of disk 3.5 mm. Arm measures 4 mm at base, 6 mm at the widest part. Genital inflation extends about 13.5 mm. Female. Paratypes: RSIOAST0112 & RSIOAST0113, disks absent, seven detached arms mixed in one jar. Longest arm measures about 230 mm. Arm 4.1 mm wide at base,

4.7 mm at the widest part. Genital inflation extends about 16 mm. Female.

Abactinal surface of disk with small rounded plates, each with one short spinelet measuring about 0.2 mm in length (Fig. 2B). At the base of the spinelets is a circle of 2–6 small pedicellariae, less than 0.1 mm in length. Spinelets are more crowded and longer at center of the

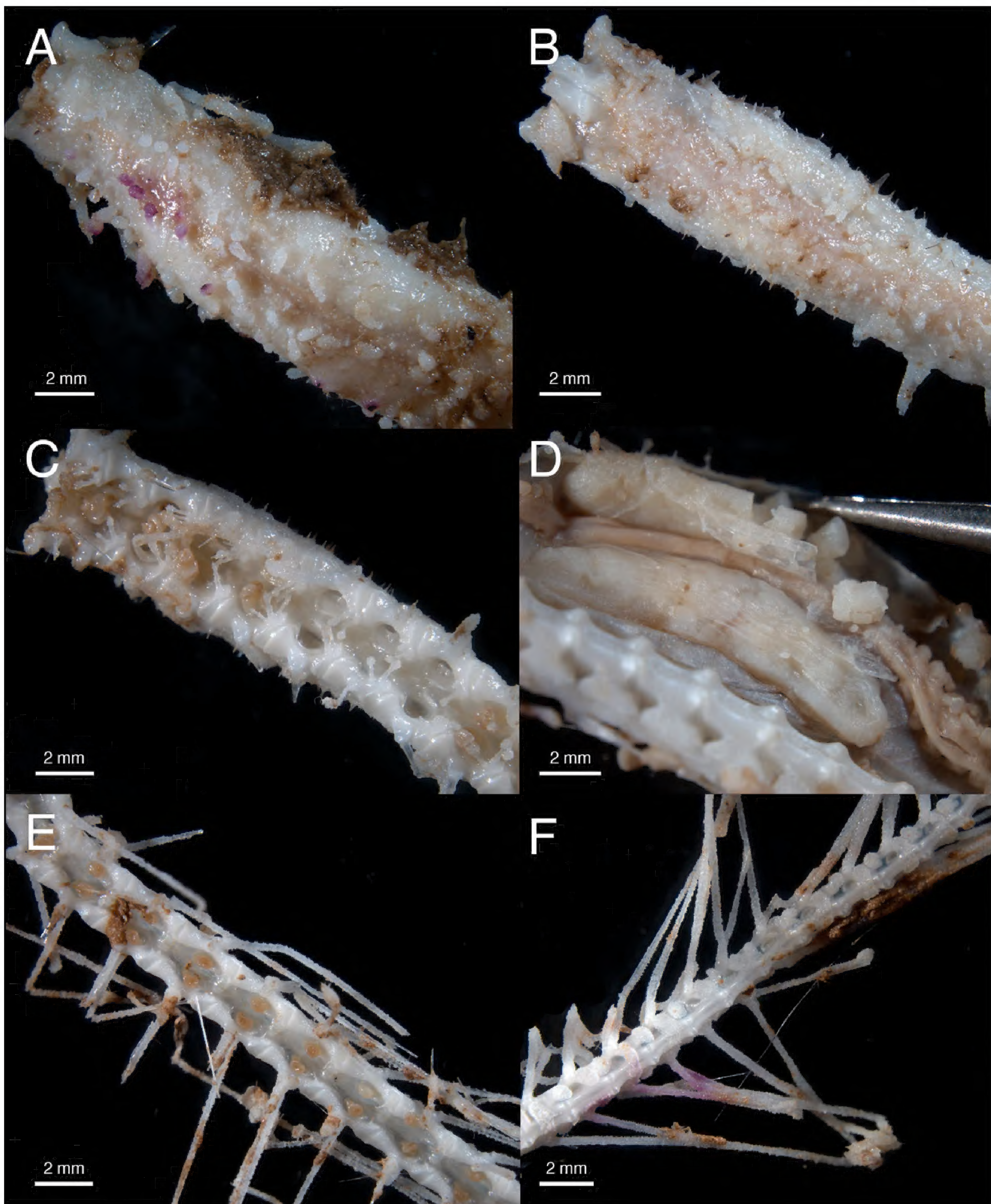


Figure 4. *Freyastera jiaolongi* sp. nov. paratypes. **A, D.** RSIOAST0112; **B, C, E, F.** RSIOAST0AS113. **A, B.** Abactinal view of arm in genital area; **C.** Actinal view of arm in genital area; **D.** Female gonads; **E.** Actinal view of middle part of arm; **F.** Abactinal view of middle part of arm.

disk, where the anus located but obscured by a cluster of spinelets. Madreporite with a subcentral cleavage, 1.3 mm in diameter, rather large and protruding, situated near the interradian margin of the disk above the odontophore. The surface of madreporite also covered with spinelets and small pedicellariae.

Basal part of arm with slight genital inflation. A pair of gonads to each arm. Female gonads encapsulated in a long sac, about 13 mm in length (Fig. 4D). Abactinal armature of arm in the genital area with irregular polygonal-shaped plates, much larger than those on disk (Fig. 2D). Each plate carries one short spine, about

0.5–0.8 mm in length, covered with a tegument loaded with minute pedicellariae (Figs 2D, 3A, 4A, B). A minority of larger plates carry two or even three spines. The surface of arm plates also scattered with small pedicellariae. The abactinal plates do not seem to go far beyond genital area. The spines become shorter at the end of genital area, sheathed with pedicellariae-covered tegument (Fig. 3B, C). Beyond genital area, the pedicellariae cluster in round tegumentary pads (Fig. 3D). At the distal part of the arm, pedicellariae pads or transverse bands occur alternately (Figs 3E, F, 4F).

Adambulacral plate narrow and elongated (Figs 2C, E, 4C). Each bearing one central subambulacral spine and 1–3 small aboral furrow spines. Furrow spines at the base of arm measure less than 1 mm in length, covered with a few scattered small pedicellariae and usually a tuft of pedicellariae at the tip. Furrow spines become fewer and smaller at middle to distal part of arm (Fig. 4E), then disappear. Subambulacral spines sheathed, covered with dense small pedicellariae. Subambulacral spines about 2–2.5 mm in length at base of arm, 4–5 mm at middle part of arm. The first inferomarginal plate occurs at about the 7th adambulacral plate, corresponding to alternate or every third adambulacral plate within the genital area and then to every adambulacral plate beyond about 20th adambulacral. Inferomarginal plates each bear one long sheathed lateral spine, similar in form to subambulacral spines but much longer, about 20 mm in length at middle part of arm.

Oral plate with 3–4 spines in total (Fig. 2A). One or two actinostomal spines along the proximal margin of the plate, about 1 mm in length. One suboral spine, the most robust of all oral spines, 1.5–2 mm in length, situated not at the center of the plate but near the proximal-furrow margin. One aboral spine similar in size to the actinostomal spine, sitting at the distal furrow margin of the plate. All mouth spines with pointed or obtuse tips, covered with minute pedicellariae.

A small crustacean skeleton found in the mouth of the holotype (Fig. 2A).

Etymology. Named after the Chinese manned submersible *Jiaolong* that collected all three specimens of the new species.

Distribution. Northwest Pacific: Kyushu-Palau Ridge. 3523–3641 m.

Remarks. The new species is morphologically most similar to the type species of the genus, *Freyastera sexradiata*, in the armature of abactinal arm plate, adambulacral plate, and oral plate. It differs from *F. sexradiata* mainly in the armature of abactinal disk. In *F. sexradiata* ($r = 6$ mm), the abactinal surface of disk bears “fairly elongated spines,” and pedicellariae are absent from the disk (Perrier, 1894). In the new species ($r = 5.5$ mm), the abactinal surface of disk is equipped with small hirsute spinelets, about 0.2 mm in length, which are circled by numerous small pedicellariae. The two species are also geographically distant (Fig. 1). *F. sexradiata* is known from the North Atlantic, whereas the new species is distributed in the Kyushu-Palau Ridge in the Philippine Sea. Genetically, the new species is close

to another undescribed species, *Freyastera* sp. 5 (COI distance 2.64%–3.52%). The latter was not described here as only fragmented arms were collected, but in these arm fragments, none of the adambulacral plates bear any furrow spines, which is distinguishable from the new species.

Freyastera sexradiata (Perrier, 1885)

Freyella sexradiata: Perrier 1885: 6; 1894: 89; Koehler 1909: 129; Grieg 1921: 30; Mortensen 1927: 129; Fisher 1928: 24; Madsen 1951: 84; Cherbonnier and Sibuet 1972: 1356; Korovchinsky and Galkin 1984: 1213 (in key); Galkin and Korovchinsky 1984: 167.

Freyellidea sexradiata: Fisher 1917: 429.

Freyastera sexradiata: Downey 1986: 40; Clark and Downey 1992: 481; Mah 1998: 87; Mah in Clark and Mah 2001: 318; Dilman 2014: 38; Zhang et al. 2019: 6 (in key).

Material examined. MNHN-IE-2014-165 (*holotype*). MOM-81 0428. (Suppl. material 1).

Diagnosis. Arms six. Abactinal disk plate, each with one fairly elongated spine. Pedicellariae absent on abactinal disk. Abactinal arm plates each bears one spine, covered with a membranous sheath loaded with small pedicellariae. Each adambulacral plate with one small aboral furrow spine and one subambulacral spine. Lateral spines corresponding to each adambulacral plate beyond genital area. Oral plate with two actinostomal spines, one suboral spine, and one aboral spine along the furrow margin.

Distribution. North Atlantic, 4020–5110 m. Type locality: Between the Azores and France, 4060 m.

Remarks. *F. sexradiata* is the type species of the genus. The holotype was examined in the present study, which demonstrates the key characters of the species as described by Perrier (1885, 1894), including having abactinal arm plate with one long spine, adambulacral plate with one subambulacral spine and one small aboral furrow spine, oral plate with two actinostomal spines, one suboral spine, and one aboral furrow spine. The arrangement of inferomarginal plates was not described in *F. sexradiata* (Perrier, 1885, 1894), and the holotype was too broken to be examined for such a character. Based on the drawings in Perrier (1894), the inferomarginal plates appear at each adambulacral plate beyond genital area. Another specimen examined (MOM-81 0428) also has continuous inferomarginal plates beyond genital area. The photos of the holotype of *F. sexradiata* are available on the MNHN collection website (holotype: <https://science.mnhn.fr/institution/mnhn/collection/ie/item/2014-165>).

Freyastera delicata Zhang et al., 2019

Figs 5, 14D

Freyastera delicata: Zhang et al. 2019: 2; Zhang et al. 2024: 10.

Material examined. RSIOAST0022 (*holotype*). RSIOAST0135 (Figs 5, 14D). (Suppl. material 1).

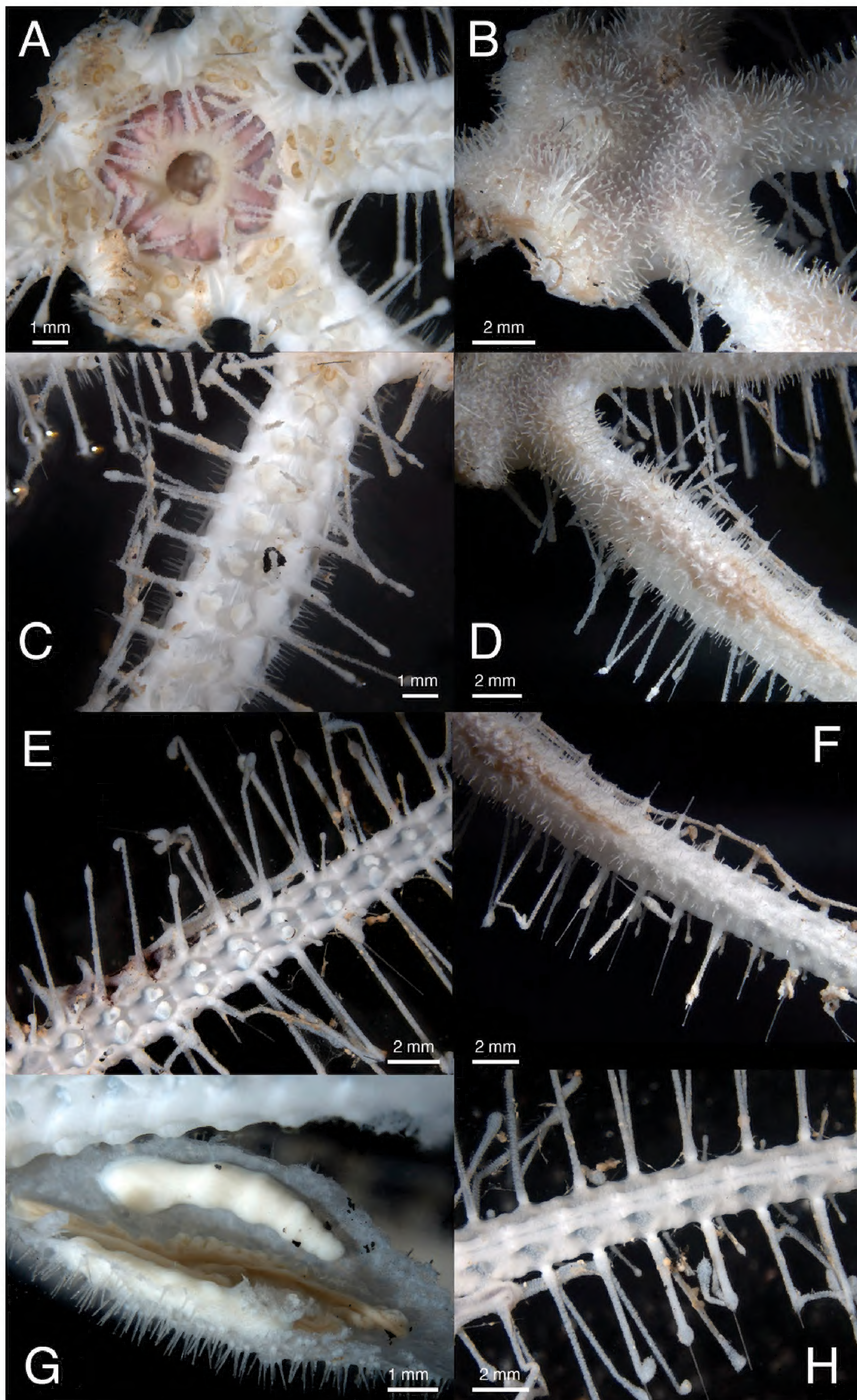


Figure 5. *Freyastera delicata* Zhang et al., 2019, RSIOAST0135. **A.** Actinal view of disk; **B.** Abactinal view of disk; **C.** Actinal view of arm genital area; **D.** Abactinal view of genital area; **E.** Actinal view of middle part of arm; **F.** Abactinal view of arm beyond genital area; **G.** Female gonads; **H.** abactinal view of middle part of arm.

Diagnosis. Arms six. Abactinal disk and arm plate each bears multiple spines (usually 4–8), most measuring 0.5–0.8 mm in length, not covered by membranous sheath. Pedicellariae absent on abactinal surface of disk and arm genital area. Pedicellariae cluster in transverse bands on abactinal arm beyond genital area. One long aboral spine and one subambulacral spine on each adambulacral plate. Proximal subambulacral spines with truncate end. Lateral spine corresponds to every adambulacral plate beyond genital area. Oral plate bears two actinostomal spines, one suboral spine, and one aboral furrow spine.

Distribution. Northwest Pacific: Caiwei Seamount, O-Hakuchō Guyot, 3121–4322 m. Type locality: Caiwei Seamount, 4322 m.

Remarks. The species was described based on a single specimen (holotype RSIOAST0022) (Zhang et al. 2019). An additional specimen was examined in the present study, providing information on intraspecific variations of the species. The specimen RSIOAST0135 (Fig. 5) is smaller compared to the holotype, with maximum $R = 135$ mm, $r = 4.1$ mm, $R/r \approx 33$. The arm measures 3.5 mm wide at the base, whereas the widest part of arm measures 4.6 mm. The genital area is about 9.5 mm in length. Gonads well-developed, female (Fig. 5G). Abactinal arm spines slightly longer than those in the holotype, but not aligned in transverse rows as in the holotype (Fig. 5D). The new specimen shares other characters with the holotype, including having no trace of pedicellariae on abactinal disk and genital area (Fig. 5B, D), mouth plate with two actinostomal spines, one suboral spine, and one aboral furrow spine (Fig. 5A), adambulacral plate with one subambulacral spine and one aboral spine pointing upwardly (Fig. 5C, E), abactinal arm plate with several spines, and arm beyond genital area with transverse bands of pedicellariae (Fig. 5H). The new specimen was found at 3121 m depth from O-Hakuchō Guyot, close to the type locality (Fig. 1), but is 1201 m shallower than the depth of the holotype (4322 m).

Freyastera basketa Zhang et al., 2019

Figs 6, 14E

Freyastera basketa: Zhang et al. 2019: 4; Zhang et al. 2024: 2,

Material examined. RSIOAST0038 (*holotype*). RSIOAST0006 (*paratype*); RSIOAST0008 (*paratype*); RSIOAST0039 (*paratype*). RSIOAST0200 (Figs 6A–F, 14E); RSIOAST0201 (Fig. 6 G, H); NHMUK 8963; SO268-2_174_116. (Suppl. material 1).

Diagnosis. Arms 6. Abactinal disk and arm plate each bears one long, sharp spine, about 1 mm in length, not covered by membranous sheath. Enlarged pedicellariae (about 0.3–0.5 mm in length) with curved valves present on oral spines and abactinal surface of disk and arm genital area. Small pedicellariae (less than 0.2 mm in length) cluster in transverse bands on abactinal arm beyond genital area. One aboral furrow spine and one

subambulacral spine on each adambulacral plate. Proximal subambulacral spines with truncate end. One lateral spine corresponding to every adambulacral plate beyond genital area. Oral plate bears one actinostomal spine, one suboral spine, and one furrow spine, all covered by large pedicellariae.

Distribution. Northwest Pacific: Mariana Trench, Yap Trench, Lamont Seamount, Pigafetta Basin; Eastern Pacific: Clarion-Clipperton Zone (CCZ). 4137–4991 m. Type locality: Mariana Trench, Yap Trench, Lamont Seamount, 4798–4991 m.

Remarks. This species is characterized by having enlarged pedicellariae with curved valves on oral spines and abactinal surface of disk and arm genital area (Fig. 6A, B, G), and one long, unsheathed spine on each abactinal arm plate. In some specimens, the proximal adambulacral spines are also equipped with large pedicellariae. The large pedicellariae are found in other *Brisingida* species, such as *Freyella macropedicellaria* Korovchinsky & Galkin, 1984; *Freyella remex* Sladen, 1889; and *Astrocles japonicus* (Korovchinsky 1976), as well as *Freyellaster* species (Zhang et al. 2024). In *Freyastera*, only *F. basketa* and *F. mortenseni* were found to have large pedicellariae. *F. basketa* has rather long, sharp spines on abactinal disk and arms, one to each plate, whereas *F. mortenseni* has several spines on each plate. Furthermore, *F. mortenseni* was reported at greater depth (5850 to 6200 m) than *F. basketa* (4137 to 4991 m). The newly examined specimens extend the distribution range of *F. basketa* to CCZ in the Eastern Pacific (Fig. 1).

Freyastera mortenseni (Madsen, 1956)

Fig. 7

Freyella mortenseni: Madsen 1956: 29; Korovchinsky and Galkin 1984: 1213 (in key); Galkin and Korovchinsky 1984: 166; Mah in Clark and Mah 2001: 322.

Freyastera mortenseni: McKnight 2006: 81; Zhang et al. 2019 (in key); Mah 2022: 15.

Material examined. RSIOAST0102 (Fig. 7); IDSSE-EEB-HX02. (Suppl. material 1).

Diagnosis. Arms 6. Abactinal disk scattered with long, sharp spines. Abactinal arm plates with 1–5 (usually 2–4) spines of similar size and form with those on disk, not covered by membranous sheath. Abactinal arm plates and spines extend beyond genital area. Enlarged pedicellariae (about 0.5 mm in length) with curved valves present on oral spines, proximal adambulacral spines, abactinal surface of disk, and arm genital areas. Small pedicellariae (about 0.1 mm in length) cluster in transverse bands on abactinal arm beyond genital area. Proximal adambulacral plates with one subambulacral spine, one aboral spine, and one furrow spine in a diagonal row. Proximal subambulacral spines with truncate end. Oral plate with one actinostomal spine, one suboral spine, and one aboral furrow spine.

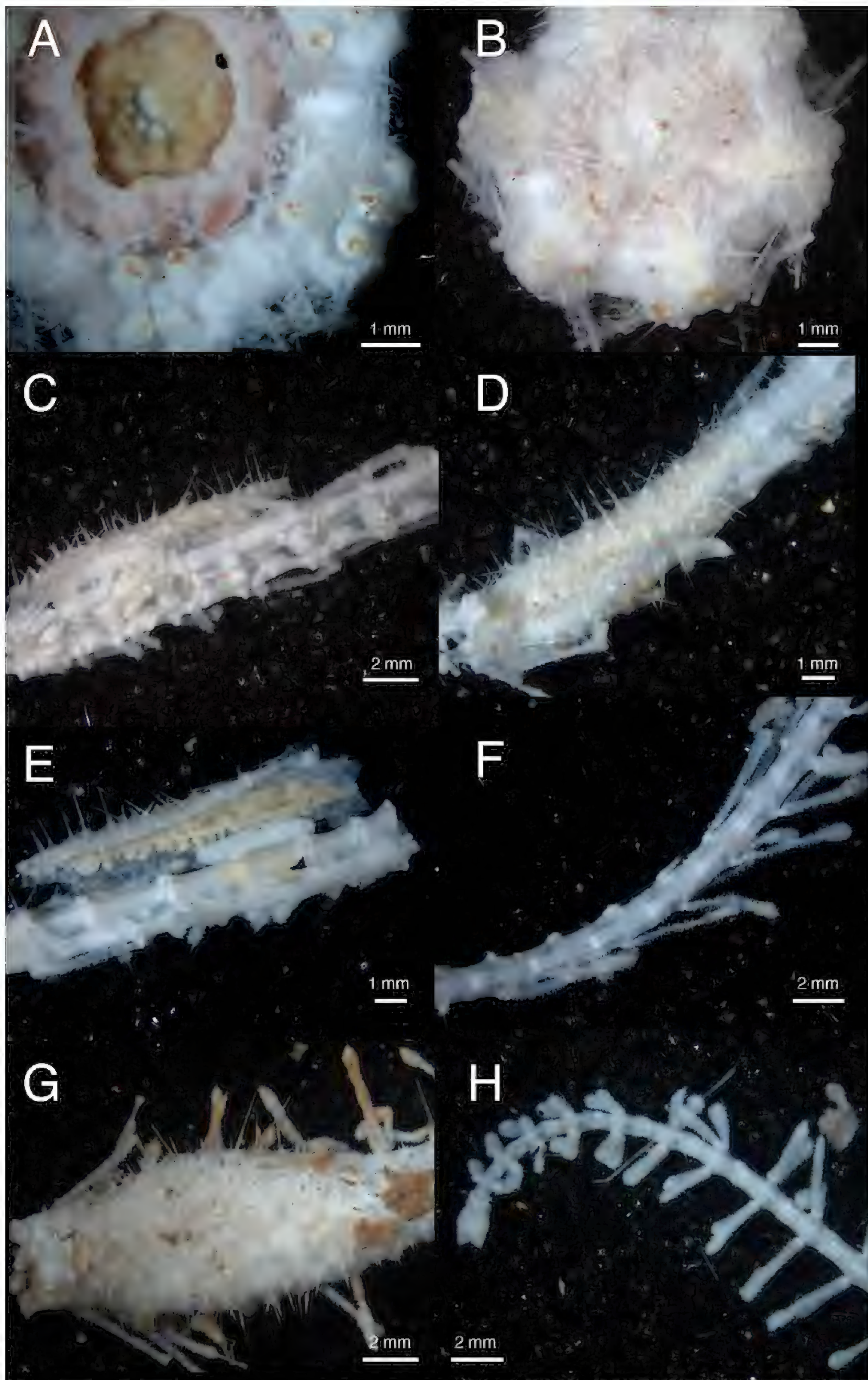


Figure 6. *Freyastera basketa* Zhang et al., 2019. **A–F.** RSIOAST0200; **G–H.** RSIOAST0201. **A.** Actinal view of disk; **B.** Abactinal view of disk; **C.** Actinal view of arm genital area; **D.** Abactinal view of genital area; **E.** Female gonad; **F.** Abactinal view of distal part of arm; **G.** Actinal view of arm genital area; **H.** Distalmost part of arm.

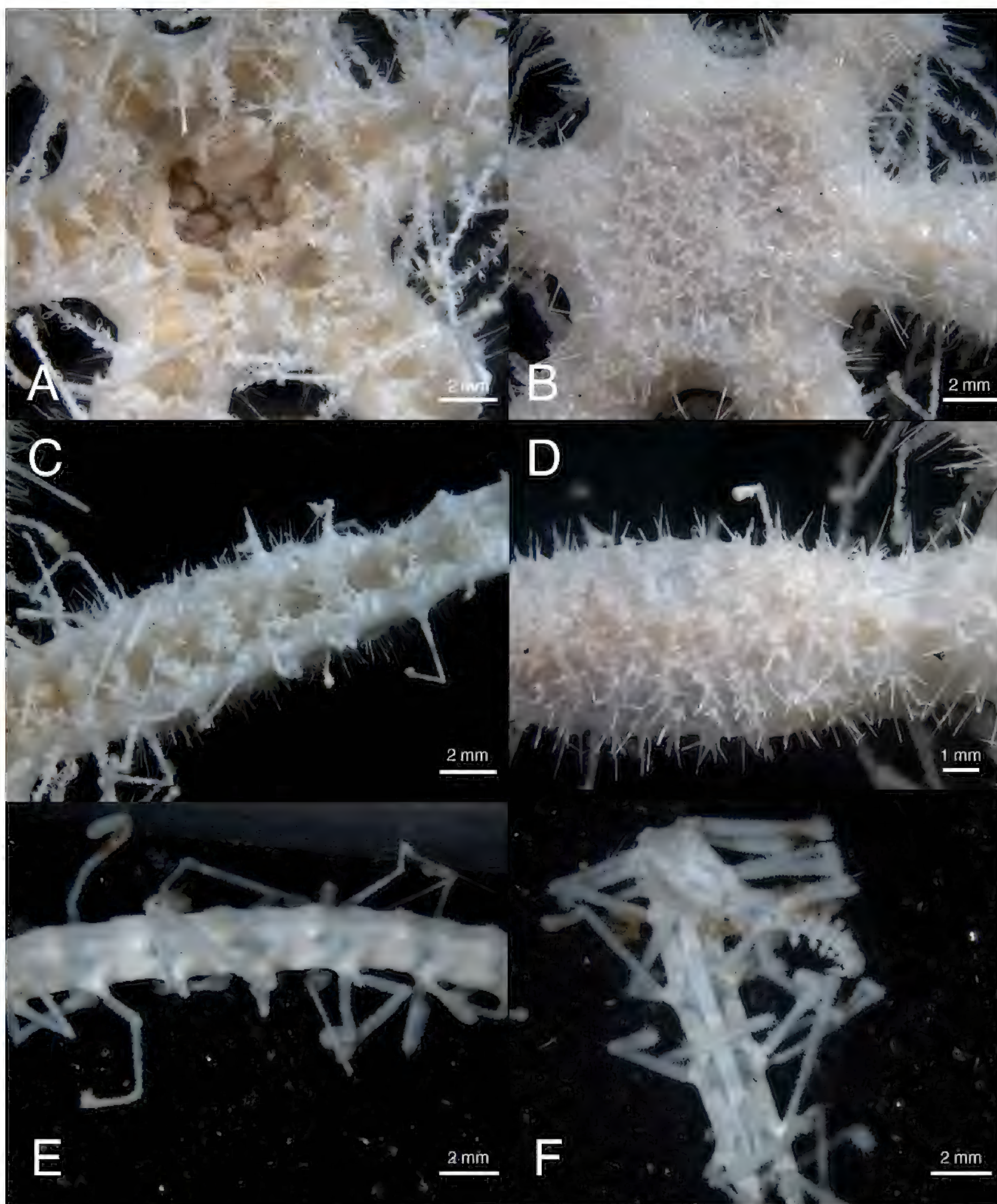


Figure 7. *Freyastera mortenseni* Madsen, 1956, RSIOAST0102. **A.** Actinal view of disk; **B.** Abactinal view of disk; **C.** Actinal view of arm genital area; **D.** Abactinal view of arm genital area; **E.** Abactinal view of middle part of arm; **F.** Distalmost part of arm, tip regenerating.

Distribution. Southwest Pacific: Kermadec Trench; Northwest Pacific: Mariana Trench, Parece Vela basin. 5850–6200 m. Type locality: Kermadec Trench, 5850 m.

Remarks. *F. mortenseni* is characterized by the presence of large pedicellariae on abactinal disk and arm genital area, as well as on oral spines and proximal adambulacral spines (Fig. 7A, B, D). The adambulacral plate of the species carries one subambulacral spine and two aboral spines in an oblique row (Fig. 7C). Beyond genital area,

the large pedicellariae are absent; instead, small pedicellariae form transverse bands (Fig. 7E, F). This species is morphologically and phylogenetically close to *F. basketa* (Fig. 12), which also possesses large pedicellariae. The newly examined specimens extend the geographical and depth range of *F. mortenseni*, representing one of the deepest occurrences of *Freyastera*. *F. mortenseni* was also reported in the American Samoa region at 3770 m depth (Mah 2022). However, based on the photos of the specimen investigated

(Mah 2022, Fig. 4C), the large pedicellariae were not present on the oral spines. This specimen, with 1–4 (usually 2–3) sharp spinelets on abactinal plate, three adambulacral spines in a diagonal row, absence of large pedicellariae (based on photo and description), and presence of small pedicellariae on abactinal plates, is potentially a new species that is close to *F. mortenseni* and *F. delicata*.

Freyastera mexicana (A.H. Clark, 1939)

Freyella mexicana: A.H. Clark 1939: 442; Korovchinsky and Galkin 1984:1213 (in key).

Freyastera mexicana: Downey 1986: 38; Clark and Downey 1992: 481; Mah 1998: 87; Mah in Clark and Mah 2001: 318; Pawson et al. 2009: 1191; Zhang et al. 2019 (in key).

Diagnosis (revised from A.H. Clark 1939). Arms six. Abactinal disk plate, each with a single spinelet. Genital region uniformly covered with larger plates, each with usually 2–4 similar spinelets, more or less in a transverse series. Pedicellariae numerous on disk and arms. Each mouth plate with 9–12 spines. First two adambulacral plates united by syzygy. Proximal adambulacrals with a diagonal row of 4 or 5 spines.

Distribution. Only known at type locality: Gulf of Mexico, 2683 m.

Remarks. No specimens of *Freyastera mexicana* were examined in the present study. However, the high-resolution photos of the holotype (USNM E 5602) are available on the collection website of the National Museum of Natural History, US (<https://collections.nmnh.si.edu/>), allowing for a rough observation of some important characters. The species has a few peculiar characters as described by A.H. Clark (1939), including having a “small unpaired interradial plate between the upper ends of the mouth plates of each pair,” the first two adambulacral plates united by syzygy, and a high number of oral spines (9–12). These characters are not common in *Freyastera* or even Freyellidae. Judging from the photos of the holotype, the specimen is generally *Freyastera*-like. Although A.H. Clark noted that the species resembles *Colpaster scutigerula* Sladen, 1889, the most, it does not have the same “inter-radial plate” (actually inferomarginal plate; see Zhang et al. 2024) inserting in between the mouth plates as in *C. scutigerula*. The oral spines do not seem to be as numerous as described, but this could be owing to damages during examination and long-time preservation. This species resembles *F. delicata* the most but differs from the latter by having numerous small pedicellariae on abactinal disk and arms, as well as having more spines on oral and adambulacral plates. Furthermore, the “syzygy” between the first and second adambulacral plates seems to be obvious from the photos. This structure, redefined as a “partial fusion” by Zhang et al. (2024), was thought to be a character only present in Brisingidae and Brisingasteridae. The nature of such a structure observed in *F. mexicana* needs to be further evaluated to be compared with the partial fusion found in Brisingidae and Brisingasteridae.

Freyastera tuberculata species complex

Diagnosis of the species complex. Arms six. Abactinal disk and arm plate each bears one spine, covered with a membranous sheath loaded with small pedicellariae. Abactinal arm plates extend beyond genital area to over middle part of the arm. Beyond that, small pedicellariae cluster in pads or transverse bands. All pedicellariae small (less than 0.2 mm in length). Adambulacral plate with one subambulacral spine only, furrow spine absent, except in one specimen of *F. giardi*, a few proximal plates with one furrow spine (see Remarks). Oral plate usually with one actinostomal spine and one suboral spine. An additional actinostomal spine and/or aboral spine along the furrow margin may present.

Remarks. The *Freyastera tuberculata* species complex discussed herein includes three known species, *Freyastera giardi* comb. nov., *Freyastera loricata* comb. nov., and *Freyastera tuberculata*, and three undescribed species, *Freyastera* cf. *tuberculata*, *Freyastera* sp. 2, and *Freyastera* sp. 7.

F. giardi and *F. loricata*, which used to be classified as *Freyella*, are reassigned here to *Freyastera*, as they have inferomarginal plates generally corresponding to every adambulacral plate beyond genital area (Koehler 1908; Korovchinsky and Galkin 1984). They also show similar morphological characters with *F. tuberculata*, which are distinctive from the other *Freyastera* species. These characters include: 1) abactinal disk and arm plate each bear one spine, sheathed and covered with small pedicellariae (Figs 8A, C, 9A, C, E, G); 2) abactinal arm plate extends beyond genital area to over middle part of the arm (Figs 8E, 9I); 3) adambulacral plate absent of furrow spine (only a few proximal plates with one furrow spine in *F. giardi*) (Figs 8F, 9D, H); 4) large pedicellariae absent. It needs to be noted that, in the four syntype specimens of *F. giardi*, only one specimen has furrow spines at a few proximal adambulacral plates (Fig. 8F) (also noted by Koehler 1908). In the other syntype specimens, the furrow spine is absent. The presence of a few furrow spines in one of the syntypes might be an abnormality. As noted by Korovchinsky and Galkin (1984), *F. loricata* is differentiated from *F. tuberculata* in the abactinal coating of arms consisting of plates of irregular shape (rather than hexagonal), the length of the abactinal spines (0.5–0.7 mm instead of 1.25 mm), and the smaller length of the adambulacral plates. However, these differences seem to be trifling, and re-examination of the types shows that the length of abactinal spines in the two species is not much different (Fig. 9A, E). Based on the original descriptions and specimens examined, the three species have rather indistinctive morphological differences and thus are considered here as a species complex. On the other hand, the three species were known from different oceans. *F. tuberculata* was described from the Atlantic; *F. giardi* was known from the Atlantic side of the Southern Ocean; and *F. loricata* was found in the Northwest Pacific near the Kuril-Kamchatka Trench (Fig. 1). Such a great geographical distance may

support them as different species, but to understand the morphological variations among them, more specimens preserved in good conditions need to be studied.

Furthermore, several newly collected specimens examined in the present study were found to have similar morphological characters to the three species above. These include five specimens identified as *Freyastera* cf. *tuberculata* from CCZ (Glover et al. 2016; Amon et al. 2017; Bribiesca-Contreras et al. 2022), a specimen identified as *Freyastera tuberculata* from the Southern Ocean (Moreau et al. 2015, 2018) (here referred to as *Freyastera* sp. 7), and two specimens temporarily named *Freyastera* sp. 2 from CCZ (Bribiesca-Contreras et al. 2022) and the Philippine Sea. *Freyastera* sp. 7 was collected near the type locality of *F. giardi* in the Southern Ocean (Fig. 1), but with only arm fragments, hindering a proper comparison of it with other species. *Freyastera* cf. *tuberculata* and *Freyastera* sp. 2 are genetically close (COI distance 2.73%–3.78%) and were collected from close sites in the CCZ (Fig. 1). A close examination of the specimens fails to identify clear, distinctive morphological differences. As noted by Bribiesca-Contreras et al. (2022), the abactinal disk spines of *Freyastera* cf. *tuberculata* seem to be shorter than those in *Freyastera* sp. 2 (Fig. 10). Although species delimitation results based on genetic data indicate that they should be considered as separate species, more subtle morphological characters or inner skeleton characters need to be examined to know the morphological differences between *Freyastera* cf. *tuberculata* and *Freyastera* sp. 2, which in turn will help to set the boundaries among the species in the *F. tuberculata* species complex.

Freyastera giardi (Koehler, 1907), **comb. nov.**

Fig. 8

Freyella giardi: Koehler 1907: 145; 1908: 242; Fisher 1940: 75; A.M. Clark 1962: 68; Korovchinsky and Galkin 1984: 1213 (in key); Mah 1998: 89; Mah in Clark and Mah 2001: 321; Moreau et al. 2015: 8; Moreau et al. 2018: 147; Zhang et al. 2019: 6 (in key).

Material examined. NHMUK 1912.11.11.30 (**syntype**) (Fig. 8A–E); MNHN-IE-2014-463 (**syntype**) (Fig. 8F); MOM-INV-0021953 (**syntype**). (Suppl. material 1).

Remarks. *Freyella giardi* was first proposed by Koehler (1907) and described in detail later by the same author (Koehler 1908). As a six-armed species, Koehler (1908) remarked upon its affinity to *F. sexradiata* but did not compare it with *F. tuberculata*. According to the original description and examination of the syntypes, this species has inferomarginal plates and lateral spines generally corresponding to every adambulacral plate beyond genital area. Based on this character and many other characters that *F. giardi* shared with *F. tuberculata* as discussed above, we reassign this species as *Freyastera giardi* **comb. nov.**

Distribution. Only known at type locality. Weddell Sea. 4572–4791 m.

Freyastera loricata (Korovchinsky & Galkin, 1984), **comb. nov.**

Fig. 9A–D

Freyella loricata: Korovchinsky and Galkin 1984: 1208; Galkin and Korovchinsky 1984: 167; Mah 1998: 90; Mah in Clark and Mah 2001: 322; Zhang et al. 2019: 7 (in key).

Material examined. ECH00161 (**paratype**) (Fig. 9A–D). (Suppl. material 1).

Remarks. *Freyella loricata* was described based on multiple individuals collected from east of the Kuril-Kamchatka Trench (Korovchinsky and Galkin 1984). Same as *F. giardi*, this species was traditionally classified as *Freyella* but has many shared characters with *Freyastera*, especially with *F. tuberculata*. It has inferomarginal plates and lateral spines that begin at the 7th adambulacral plate, appear at alternate adambulacral plates, and then at every adambulacral plate (Korovchinsky and Galkin 1984); thus, we reassign this species as *Freyastera loricata* **comb. nov.**

Distribution. Only known at type locality. East of the Kuril-Kamchatka Trench. 4995–5998 m.

Freyastera tuberculata (Sladen, 1889)

Fig. 9E–I

Freyella tuberculata: Sladen 1889: 638; Alcock 1893: 121; Mortensen 1927: 129; Korovchinsky and Galkin 1984: 1214 (in key); Galkin and Korovchinsky 1984: 167.

Freyellidea tuberculata: Fisher 1917: 429; H. L. Clark 1920: 113.

Freyastera tuberculata: Downey 1986: 41; Clark and Downey 1992: 482; Mah 1998: 78; Mah in Clark and Mah 2001: 319; Moreau et al. 2015: 8; Moreau et al. 2018: 147; Zhang et al. 2019: 7 (in key).

Material examined. NHMUK 1890.5.7.1076 (**syntype**) (Fig. 9E–I); NHMUK 1890.5.7.1077 (**syntype**).

Other material. MNHN-IE-2008-1363; MNHN-IE-2017-1819; MNHN-IE-2019-5479; MNHN-IE-2019-5743; MNHN-IE-2019-5745. (Suppl. material 1).

Distribution. Atlantic Ocean; Eastern Pacific; Indian Ocean; Bay of Bengal. 3365–5180 m. Type locality: Atlantic Ocean: between Canary Islands and Cape Verde Islands; between the coast of Africa and the Island of Ascension. 4298–4390 m.

Freyastera cf. *tuberculata*

Freyastera cf. *tuberculata*: Bribiesca-Contreras et al. 2022: 42.

Freyastera cf. *benthophila*: Glover et al. 2016: 17; Amon et al. 2017: 9; GenBank (NHM_413: KU519535; KU519518; KU519550; KU519551).

Material examined. NHMUK 2022.79 (CCZ_087); NHMUK 2022.80 (CCZ_157); NHMUK 9120; NHM_413; SO268-1_64_074. (Suppl. material 1).

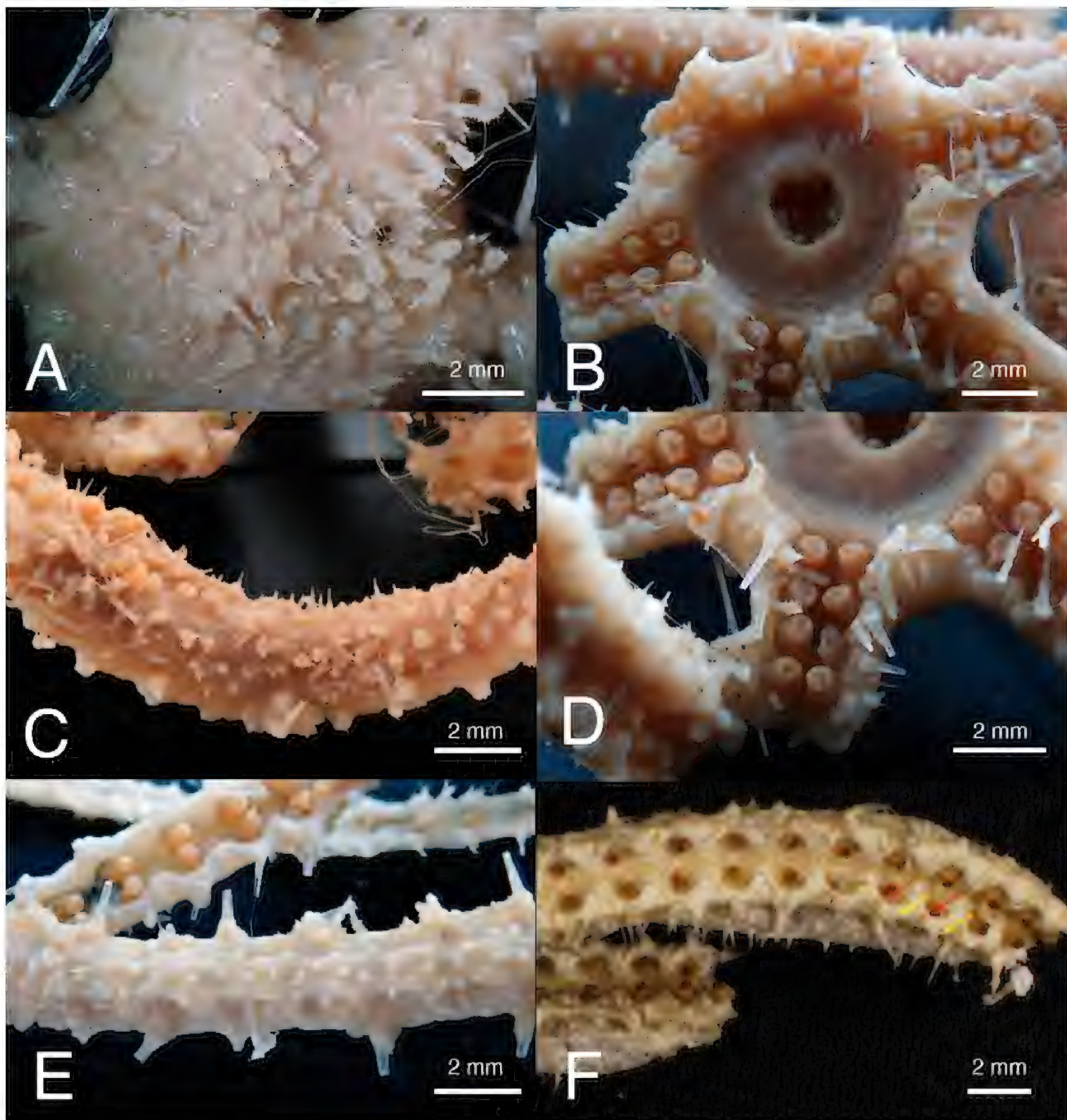


Figure 8. *Freyastera giardi* (Koehler, 1907) type specimens. **A–E.** NHMUK 1912.11.11.30; **F.** MNHN-IE-2014-463. **A.** Abactinal view of disk; **B.** Actinal view of disk; **C.** Abactinal view of arm genital area; **D.** Actinal view of disk and proximal part of arm; **E.** Abactinal view of middle part of arm; **F.** Actinal view of proximal part of arm. Yellow arrows show subambulacral spines; red arrows show aboral furrow spines.

Distribution. Eastern Pacific: Clarion-Clipperton Zone. 4011–5000 m.

Freyastera sp. 2

Fig. 10

Freyastera stet. CCZ_201: Bribiesca-Contreras et al. 2022: 44.

Material examined. NHMUK 2022.81 (Fig. 10 A, B, F) (*Freyastera* stet. CCZ_201); RSIOAST0103 (Fig. 10C–E). (Suppl. material 1).

Distribution. Eastern Pacific: Clarion-Clipperton Zone; Northwest Pacific: Western Philippine Basin. 5204–5900 m.

Freyastera sp. 7

Freyastera tuberculata: Moreau et al. 2015; Moreau et al. 2018.

Material examined. ULB_S59-MT2, multiple broken arms from different individuals. (Suppl. material 1).

Distribution. Weddle Sea, 4648 m.

Genus *Freyella* Perrier, 1885

Type species. *Freyella spinosa* Perrier, 1885, now regarded as a synonym of *Freyella elegans* (Verrill, 1884).

Diagnosis. Arms 6–15. Papulae absent. One pair of gonads on each arm. The first pair of inferomarginal

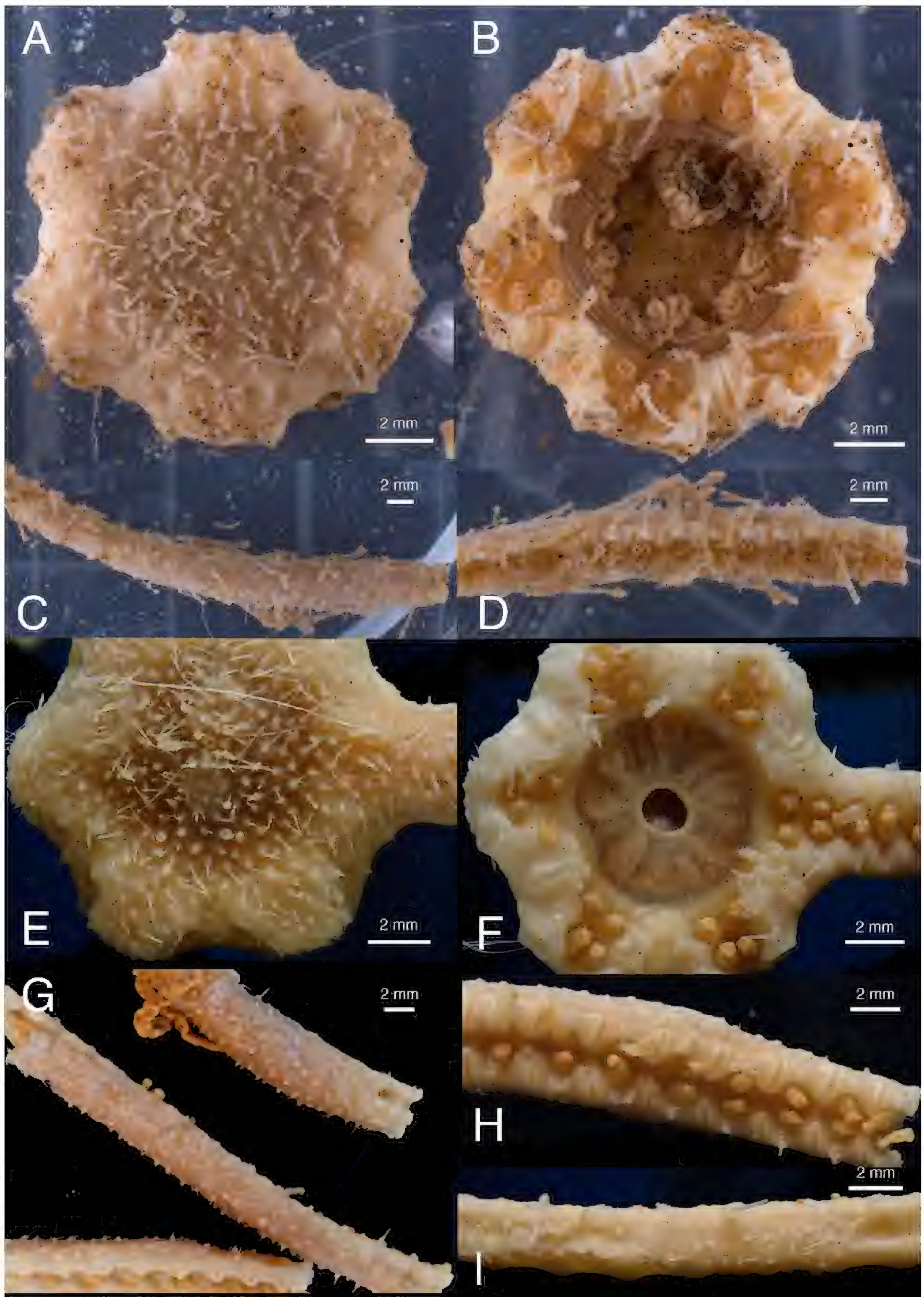


Figure 9. A–D. *Freyastera loricata* (Korovchinsky & Galkin, 1984) type ECH00161 (photos courtesy of Dr. Anna Dilman); E–I. *Freyastera tuberculata* (Sladen, 1889) type NHMUK 1890.5.7.1076. A, E. abactinal view of disk; B, F. Actinal view of disk; C, G. Abactinal view of arm genital area; D, H. Actinal view of proximal part of arm; I. abactinal view of middle part of arm.

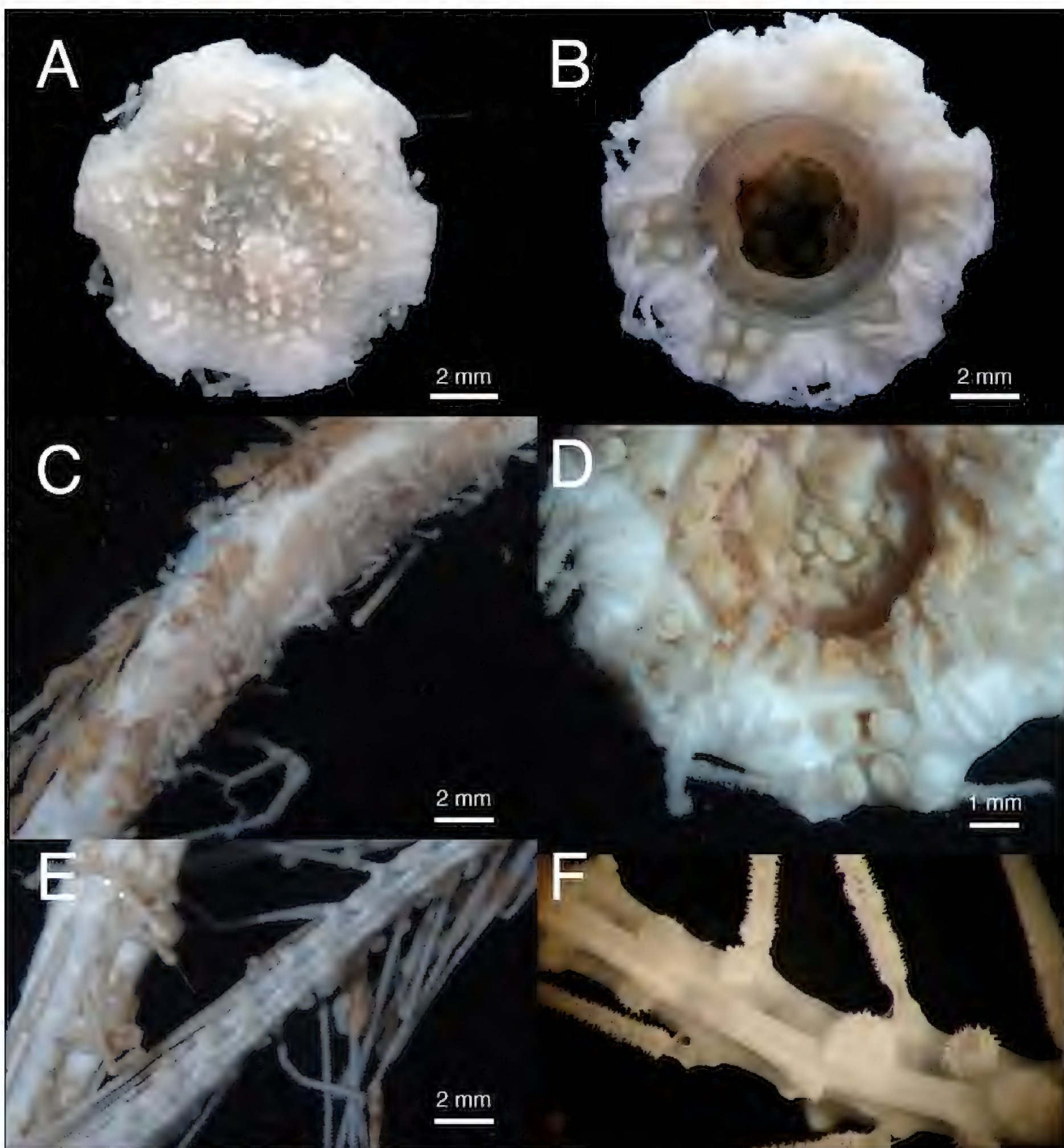


Figure 10. *Freyastera* sp. 2. **A, B, F.** NHMUK 2022.81; **C–E.** RSIOAST0103. **A.** Abactinal view of disk; **B.** Actinal view of disk; **C.** Abactinal view of arm genital area; **D.** Zoom-in view of oral plates; **E.** Abactinal view of middle part of arm; **F.** Zoom-in view of middle part of arm, showing pedicellariae clustered in small pads.

plates not in contact with the odontophore. Inferomarginal plates generally correspond to every 2nd adambulacral plate beyond genital area. Abactinal arm in genital region covered with pavement of spinate plates.

Freyella benthophila Sladen, 1889

Fig. 11

Freyella benthophila: Sladen 1889: 641; Wood-Mason and Alcock 1891: 440; Alcock 1893: 121; Fisher 1928: 24; Madsen 1951: 84; Cherbonnier and Sibuet 1972: 1356; Sibuet 1975: 292; Korovchinsky

and Galkin 1984: 1215 (in key); Galkin and Korovchinsky 1984: 165; Zhang et al. 2024: 17.

Freyellidea benthophila: Fisher 1917: 429.

Freyastera benthophila: Downey 1986: 36; McKnight 1993: 173; Mah 1998: 78; Mah in Clark and Mah 2001: 318; Dilman 2014: 38; Moreau et al. 2015: 16; Moreau et al. 2018: 147; Zhang et al. 2019: 7 (in key).

Belgicella racowitzana: Ludwig 1903: 59; Koehler 1907: 141; Koehler 1908: 245; Döderlein 1928: 293; Fisher 1928: 6; Fisher 1940: 75; A.M. Clark 1962: 68; Jangoux and Massin 1986: 91; Mah 1998: 78; Mah in Clark and Mah 2001: 317; Moreau et al. 2015: 5; Moreau et al. 2018: 147.

Material examined. NHMUK 1890.5.7.1078 (*holotype*) (Fig. 11A, B, E, G).

Other material. IA3-2168; MNHN-IE-2008-1057; MNHN-IE-2008-1073; MNHN-IE-2008-1081; MNHN-IE-2017-1829; MNHN-IE-2017-1948; MNHN-IE-2019-5752; MNHN-IE-2022-2192 (Fig. 11D); MNHN-IE-2022-2193; MNHN-IE-2022-2194; MNHN-IE-2022-2195; MNHN-IE-2022-2196; NHMUK 9237 (Fig. 11C, F, H, I); NOC 11908#44; NOC 12930#64; NOC 12930#78; NOC 13200#27; NOC 13200#60; NOC 52701#42; NOC 54901#7; NOC 54902#1; NOC 54903#1; SO268-1_29_014; SO268-2_109_189; SO268-02_99_04. (Suppl. material 1).

Diagnosis. Arms six. Abactinal armature of disk with one primary central plate at center of the disk and a primary interradiial plate at each interradius (Fig. 11A–D). Central and interradiial primary plates shield-like, much larger than the rest of abactinal disk plates (primary plates present in most specimens examined, but indistinguishable in some individuals). Abactinal disk and arm plates evenly covered with numerous short spinelets and small pedicellariae (Fig. 11G). Beyond genital area, abactinal arm with bands of small pedicellariae. Adambulacral plate with one subambulacral spine. Proximal subambulacral spines with modified tips (truncated or flattened bifurcated) (Fig. 11E, H). Furrow spine absent. Oral plate with 2–3 actinostomal spines and one suboral spine, each covered with membranous sheath, but the tips are bare (Fig. 11E, F). Spines covered with small pedicellariae. Large pedicellariae absent. Inferomarginal plates and lateral spines occur at alternate adambulacral plates beyond genital area (Fig. 11I).

Distribution. North Atlantic, Southern Pacific, Eastern Pacific, Southern Ocean. 2450–5000 m. Type locality: Southern Pacific, 4663 m.

Remarks on *F. benthophila* and other six-armed *Freyella*. *F. benthophila* stands in a peculiar position by having shared morphological characters with both *Freyastera* and *Freyella*. As a species with six arms, it is readily distinguished from other *Freyella* species with more than six arms. Compared with other *Freyastera*, it is differentiated from most species by having many small spinelets on its abactinal disk and arms and distinguished from *Freyastera mortenseni*, *F. delicata*, and *F. mexicana*, which also bears multiple spines on abactinal plates, by the absence of furrow spines and more distantly located inferomarginal plates. Phylogenetic analysis put it within the *Freyella* clade (Fig. 12; Zhang et al. 2024), indicating that having six arms is not an autapomorphy of the *Freyastera* clade.

There are three other six-armed *Freyella* species whose taxonomic position needs to be re-evaluated, including *F. oligobrachia* H.L. Clark, 1920; *F. hexactis* Baranova, 1957; and *F. vitjazi* Korovchinsky & Galkin, 1984. *F. oligobrachia* and *F. vitjazi* have inferomarginals corresponding to alternate adambulacral plates according to their original descriptions; thus, they should be retained within *Freyella*. *F. hexactis* was described to have

inferomarginal plates to every third adambulacrals, then to alternate adambulacrals, then at the end of the arm, to each adambulacral plate (Baranova 1957). It is difficult to justify it as either *Freyella* or *Freyastera* simply by this description. However, this species closely resembles *F. oligobrachia* and *F. benthophila*, as was shown in the key in Zhang et al. (2019). It is necessary to examine the types of *F. oligobrachia* and *F. hexactis* to be certain of their generic affinities and their relationship with *F. benthophila*. *F. vitjazi*, on the other hand, could be differentiated from the other six-armed *Freyella* species by having a diagonal line of three spines on each adambulacral plate. These three species are retained as *Freyella* for the time being, but they should be compared with in any future descriptions of six-armed freyellids.

Genetic distances, species delimitation, and phylogeny

The COI genetic distances among 30 *Freyastera* individuals are shown in Table 1. The distance between two specimens of the new species *F. jiaolongi* sp. nov. is 0.45%, whereas intraspecific distances of other *Freyastera* species are between 0% and 1.56%. The distances among the new species and the other *Freyastera* species are between 2.64% and 9.40%. The new species is most closely related to the undescribed species *Freyastera* sp. 5. The largest interspecific distance within *Freyastera* is 10.67%, which is found between *Freyastera mortenseni* and *Freyastera* cf. *tuberculata*.

The species delimitation tool ASAP was used for COI alignment of the 30 *Freyastera* individuals and for 16S alignment of 23 individuals. For COI alignment, a clear barcode gap was shown with the delimitation threshold value (genetic distance) found at 1.9%. The best delimitation result from COI alignment suggested 11 species (ASAP score = 2.00). The same delimitation result was yielded for the 16S alignment (11 species, ASAP score = 2.00).

The phylogenetic tree constructed in the present study (Fig. 12) shows the same topology as the tree in Zhang et al. (2024) for the *Freyastera* clade. Two clades are formed within the genus; one includes *F. basketa* and *F. mortenseni*, and the other includes the remaining nine species. However, the support values of several branches in the bigger clade are not high, especially at the branches of *Freyastera* sp. 6 and *Freyastera* sp. Yap. These two species seem to be derived from the other species and intermediate among the two clades. When only *Freyella benthophila* and *Freyella echinata* were used as outgroup, *F. sp. 6* and *F. sp. Yap* clustered with the *F. basketa* clade instead, but the support values were also very low. Another species with an uncertain position is *Freyastera* sp. 3. This species clusters with *F. jiaolongi* sp. nov. and *F. sp. 5* in the ML tree (Fig. 12), but lies outside of a cluster of *F. jiaolongi* sp. nov., *F. sp. 5*, and the *Freyastera* cf. *tuberculata* complex in the BI tree, both with low support values.

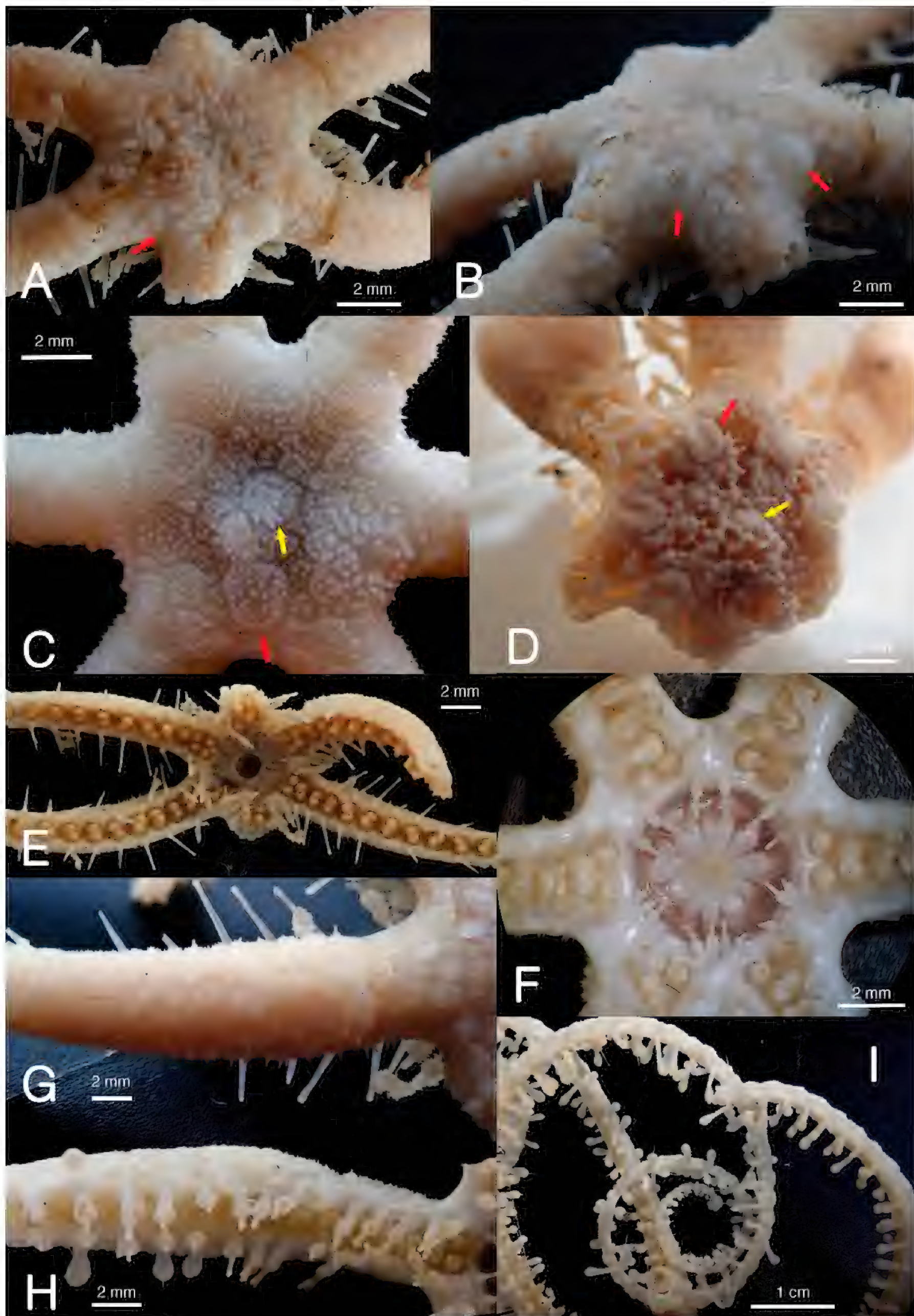


Figure 11. *Freyastera benthophila* Sladen, 1889. **A, B, F, G.** Holotype NHMUK 1890.5.7.1078; **C, F, H, I.** NHM 9237; **D.** MNHN-IE-2022-2192. **A–D.** Abactinal view of disk, red arrows show the primary interradial plates, yellow arrows show the primary central plates; **E.** Actinal view of the specimen; **F.** Actinal view of disk; **G.** Abactinal view of arm genital area, spines mostly lost; **H.** Actinal view of arm genital area; **I.** Distal part of arm.

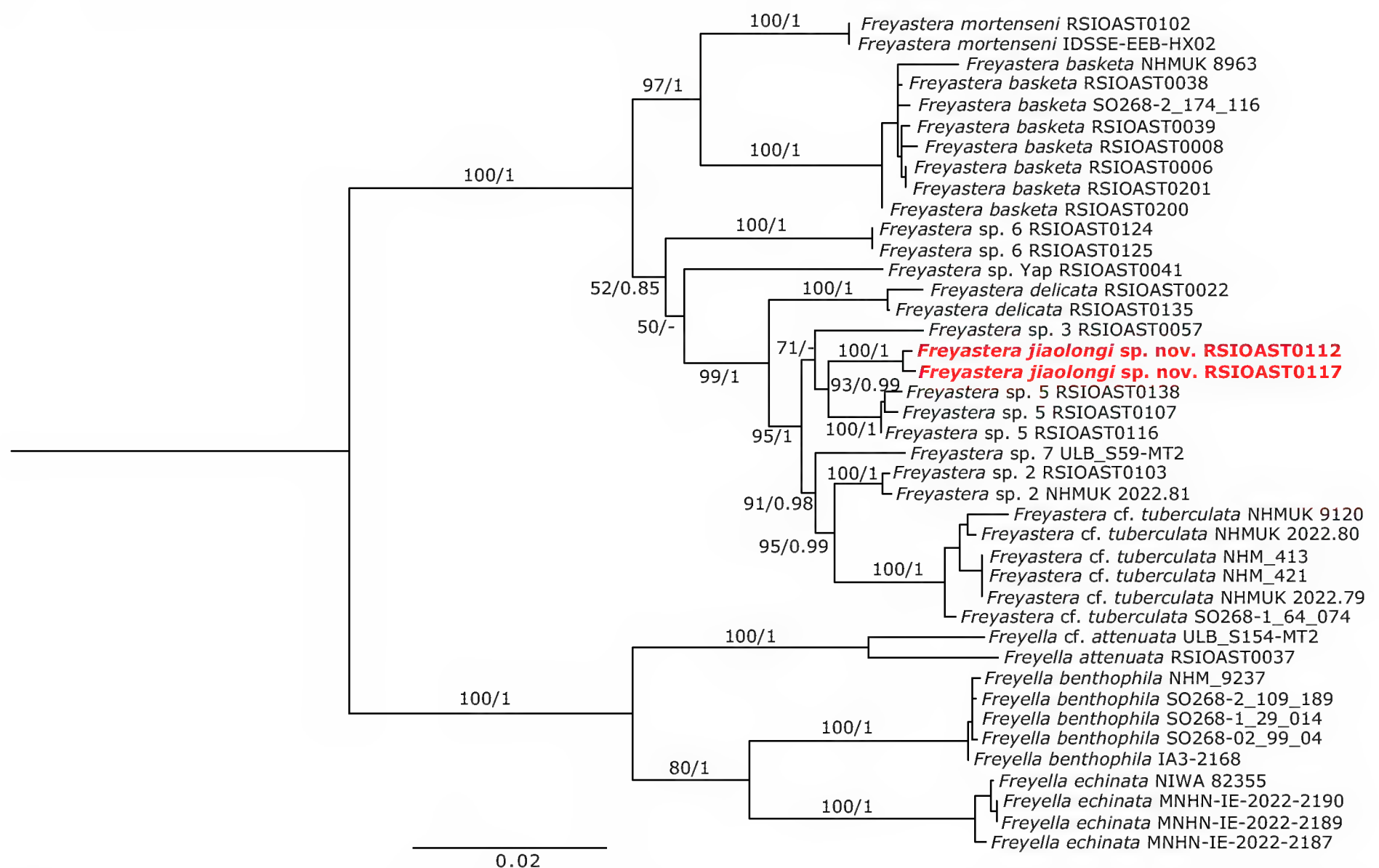


Figure 12. Phylogenetic tree of *Freyastera* using COI, 16S, 12S, and 28S concatenated dataset. Tree topology follows that of the ML tree. Numbers at each node indicate UFBS/PP support values.

Discussion

In this study, a new species, *Freyastera jiaolongi* sp. nov., is described, and two new species combinations, *Freyastera giardi* comb. nov. and *Freyastera loricata* comb. nov., are proposed. Remarks on nine *Freyastera* species and one *Freyella* species and a key to *Freyastera* species are provided based on examination of the type specimens (or photos). Molecular phylogenetic trees based on COI, 16S, 12S, and 28S genes support *Freyastera* as monophyletic and most of the inner lineages with high UFBS/PI values (Fig. 12). The new specimens examined and their genetic data allow for an investigation into the morphological and genetic boundaries among *Freyastera* species. Morphological differences among the known species were demonstrated in the systematics part. Other than the *F. tuberculata* species complex, most *Freyastera* species are well-defined and distinguishable from each other. However, several undescribed species (*Freyastera* sp. 3, *Freyastera* sp. 5, and *Freyastera* sp. 6 (Fig. 12)) were not included in the systematics as specimens were in bad condition for proper description of the species.

Genetic data showed that the COI intraspecific distances of *Freyastera* species are between 0% and 1.56%, which fall within the range of intraspecific distance of Asteroidea obtained in other studies (e.g., Ward et al. 2008; Corstorphine 2010). The interspecific distances among *Freyastera* species are between 2.64% and 10.67%. It needs to be noted that several geographically

close species have rather small interspecific distances, such as *Freyastera* cf. *tuberculata* and *Freyastera* sp. 2 (2.73%–3.78%), *Freyastera jiaolongi* sp. nov., and *Freyastera* sp. 5 (2.64%–3.52%). *Freyastera jiaolongi* sp. nov. and *Freyastera* sp. 5, as mentioned in the systematics, are distinguishable in morphology, as the former has furrow spines on adambulacral plates and oral plates, while the latter has no furrow spine at all. *Freyastera* cf. *tuberculata* and *Freyastera* sp. 2 have only subtle differences in morphology as part of the *F. tuberculata* species complex. The small interspecific distances found in these species pairs underline the complexity in the use of a universal threshold value of genetic distance to set the boundaries of species (e.g., 3% in many eDNA studies) (e.g., Laroche et al. 2020; Lanzén et al. 2021). Boundaries among species, especially less-studied deep-sea species, need to be assessed by combining different sources of evidence, including morphology, genetics, biology, and ecology.

Freyastera was believed to be distributed in the global ocean save the Arctic (Zhang et al. 2019). However, as *Freyella benthophila*, a “cosmopolitan” species, was moved out from *Freyastera*, the global distribution of *Freyastera* needs to be re-evaluated. All *Freyastera* specimens examined in the present study and the type localities are found restricted to the Pacific, Atlantic, and the Atlantic part of the Southern Ocean (Fig. 1). The presence of *Freyastera* in the Indian Ocean, on the other hand, is rather dubious. Two records of *Freyastera* were reported from the Bay of Bengal

Table 1. COI pairwise genetic distances (%) of *Freyastera* species. Distances in red color are intraspecific distances.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29
1 F. sp. Yap RSIOAST0041																													
2 F. delicata RSIOAST0022	5.46																												
3 F. delicata RSIOAST0135	5.16	0.59																											
4 F. sp. 3 RSIOAST0057	5.83	3.93	3.77																										
5 F. jiaolongi sp. nov. RSIOAST0112	6.91	5.27	5.11	3.83																									
6 F. jiaolongi sp. nov. RSIOAST0117	6.92	5.15	5.00	3.62	0.45																								
7 F. sp. 5 RSIOAST0138	6.24	4.79	4.78	3.20	3.20	3.52																							
8 F. sp. 5 RSIOAST0107	6.12	4.22	4.22	3.00	2.90	3.14	0.75																						
9 F. sp. 5 RSIOAST0116	5.73	3.92	3.92	2.80	2.64	2.96	0.77	0.31																					
10 F. sp. 7 ULB_S59-MT2	5.89	4.74	4.41	3.45	4.25	4.58	3.44	3.60	3.36																				
11 F. sp. 2 RSIOAST0103	5.96	4.22	3.91	3.93	4.79	5.01	3.82	3.60	3.59	3.11																			
12 F. sp. 2 NHMUK 2022.81	6.07	4.20	3.87	4.04	4.71	5.05	3.86	3.70	3.53	2.93	0.31																		
13 F. cf. tuberculata NHMUK 9120	9.14	7.36	7.15	5.44	6.09	6.32	6.49	6.07	5.82	4.81	3.78	3.59																	
14 F. cf. tuberculata NHM_413	7.10	5.45	5.13	4.33	5.31	5.32	5.13	4.81	4.41	2.97	3.21	2.88	1.38																
15 F. cf. tuberculata NHM_421	6.87	5.36	5.03	4.23	5.05	5.06	5.03	4.71	4.28	2.98	3.10	2.73	1.38	0.00															
16 F. cf. tuberculata NHMUK 2022.79	7.07	5.59	5.26	4.31	5.28	5.29	5.10	4.79	4.41	2.95	3.20	2.88	1.37	0.00	0.00														
17 F. cf. tuberculata SO268-1_64_074	7.40	5.62	5.31	4.24	5.28	5.49	4.78	4.37	4.08	3.27	2.83	2.88	1.17	0.90	0.76	0.90													
18 F. cf. tuberculata NHMUK 2022.80	7.91	6.24	5.91	4.79	5.77	6.11	5.26	4.94	4.57	3.43	3.35	3.04	0.97	0.75	0.76	0.75	0.75												
19 F. sp. 6 RSIOAST0124	5.63	7.24	6.59	6.62	7.73	7.90	6.89	6.91	6.38	6.37	7.41	7.10	9.31	7.76	7.35	7.72	7.72	8.05											
20 F. sp. 6 RSIOAST0125	5.74	7.22	6.55	6.55	7.73	7.89	6.89	6.89	6.38	6.37	7.38	7.10	9.31	7.76	7.35	7.72	7.71	8.05	0.00										
21 F. mortenseni RSIOAST0102	5.95	7.57	6.92	7.61	8.57	8.58	7.23	6.77	6.90	7.22	7.57	7.44	10.67	8.61	8.38	8.57	8.58	9.25	5.16	5.09									
22 F. mortenseni IDSSE-EEB-HX02	5.80	8.67	8.18	8.65	9.15	9.40	7.45	6.98	7.48	8.66	8.18	8.01	10.63	9.95	10.02	9.88	10.15	10.39	6.27	6.27	0.00								
23 F. basketa NHMUK 8963	8.47	8.88	8.44	8.20	9.31	8.88	8.63	7.98	8.24	8.43	8.44	8.30	9.34	9.82	9.88	9.99	9.97	10.20	6.94	6.94	6.48	5.57							
24 F. basketa RSIOAST0200	7.15	7.48	6.97	6.62	8.00	7.83	6.45	6.28	6.32	6.32	6.79	6.83	9.31	7.64	7.64	7.64	7.29	7.64	6.13	6.13	5.45	5.23	1.39						
25 F. basketa SO268-2_174_116	8.25	8.40	7.90	7.77	8.96	8.93	6.85	6.87	7.02	7.19	7.38	7.28	9.85	8.59	8.50	8.59	8.21	8.58	6.21	6.00	6.05	5.66	1.23	0.95					
26 F. basketa RSIOAST0038	7.75	7.89	7.41	7.12	8.25	8.23	6.24	6.27	6.56	6.55	6.92	6.93	9.55	8.28	8.22	8.24	7.88	8.23	6.45	6.25	5.81	5.10	1.17	0.62	0.61				
27 F. basketa RSIOAST0039	7.75	7.56	7.08	7.12	8.07	8.06	6.40	5.94	6.22	6.55	6.92	6.93	9.55	8.11	8.05	8.07	7.71	8.06	6.45	6.25	5.81	5.34	1.36	0.77	0.76	0.44			
28 F. basketa RSIOAST0008	7.92	7.73	7.25	7.29	8.25	8.23	6.40	6.10	6.39	6.72	7.09	7.10	9.77	8.28	8.22	8.24	7.88	8.23	6.62	6.42	5.97	5.57	1.56	0.77	0.76	0.44	0.29		
29 F. basketa RSIOAST0006	7.92	7.73	7.25	7.29	8.25	8.23	6.40	6.10	6.39	6.72	7.09	7.10	9.77	8.28	8.22	8.24	7.88	8.23	6.62	6.42	5.97	5.57	1.56	0.77	0.76	0.44	0.29	0.29	
30 F. basketa RSIOAST0201	7.95	7.93	7.39	7.56	8.65	8.48	6.85	6.32	6.68	7.03	7.20	7.12	9.79	8.10	8.10	8.10	7.91	8.09	6.52	6.52	6.16	5.87	1.43	0.80	0.80	0.48	0.32	0.32	0.00

(Alcock 1893; Shirayama and Tsuchida 1991), but no descriptions or photos of the specimens were provided. Gerdes et al. (2021) reported a *Freyastera* gen. inc. near the Edmond hydrothermal vent field in the Central Indian Ridge, but according to the photo provided, the specimen has seven arms instead of six, thus is likely to be a *Freyella*. The global distribution and bathymetrical distribution of *Freyastera* species seem to be rather restricted (Fig. 13). No species was found to have a cross-ocean distribution, and the depth range of a species is no larger than 1300 m. *F. basketa* has the widest distribution range from the Yap Trench to the eastern part of CCZ. However, this restricted distribution could also be owing to the insufficiency of data, as only 77 records were included in the map (Fig. 1).

This study reveals high species diversity of *Freyastera*, especially in the Northwest Pacific region, where ten species (including five undescribed ones) were found. On one hand, this might be owing to a greater deep-sea sampling effort in this region. Species found in this region were mostly collected from nine Chinese expeditions starting from 2013 using cutting-edge sampling vehicles such as ROV and HOV (Suppl. material 1), resulting in a fine collection of specimens for biodiversity analysis. On the other hand, the Northwest

Pacific harbors high environmental heterogeneity, providing various habitats for different species. The diversity of *Freyastera* in other regions should be further investigated with more samples to be collected in the future. Furthermore, high-resolution cameras mounted on ROV or HOV provided valuable information on the *in situ* environments of *Freyastera* species (Fig. 14). *Freyastera* have been frequently observed by submersibles and deep-tow digital cameras (e.g., Morris et al. 2014; Yu et al. 2014; Glover et al. 2016; Amon et al. 2017; Moreau et al. 2018; Zhang et al. 2019; Zhang et al. 2024; NOAA Ocean Exploration 2024) from the slope or foot of seamounts, abyssal plains, or trenches. Although living at great depth below 3000 m, they were mostly spotted attaching to hard substrate, even when the gross substrate of the environment is soft sediment (Fig. 14A–C, F). *Freyastera* sp. Yap and *Freyastera* sp. 2, on the other hand, might be directly attaching to soft sediment as shown in *in situ* photos (Zhang et al. 2019; Bribiesca-Contreras et al. 2022). Some species, namely, *F. basketa* and *F. cf. tuberculata*, were known to be associated with polymetallic nodules in either the CCZ or the Pigafetta basin (Fig. 14E) (Zhang et al. 2019; Glover et al. 2016; Amon et al. 2017; Bribiesca-Contreras et al. 2022), but such an association is not obligate,

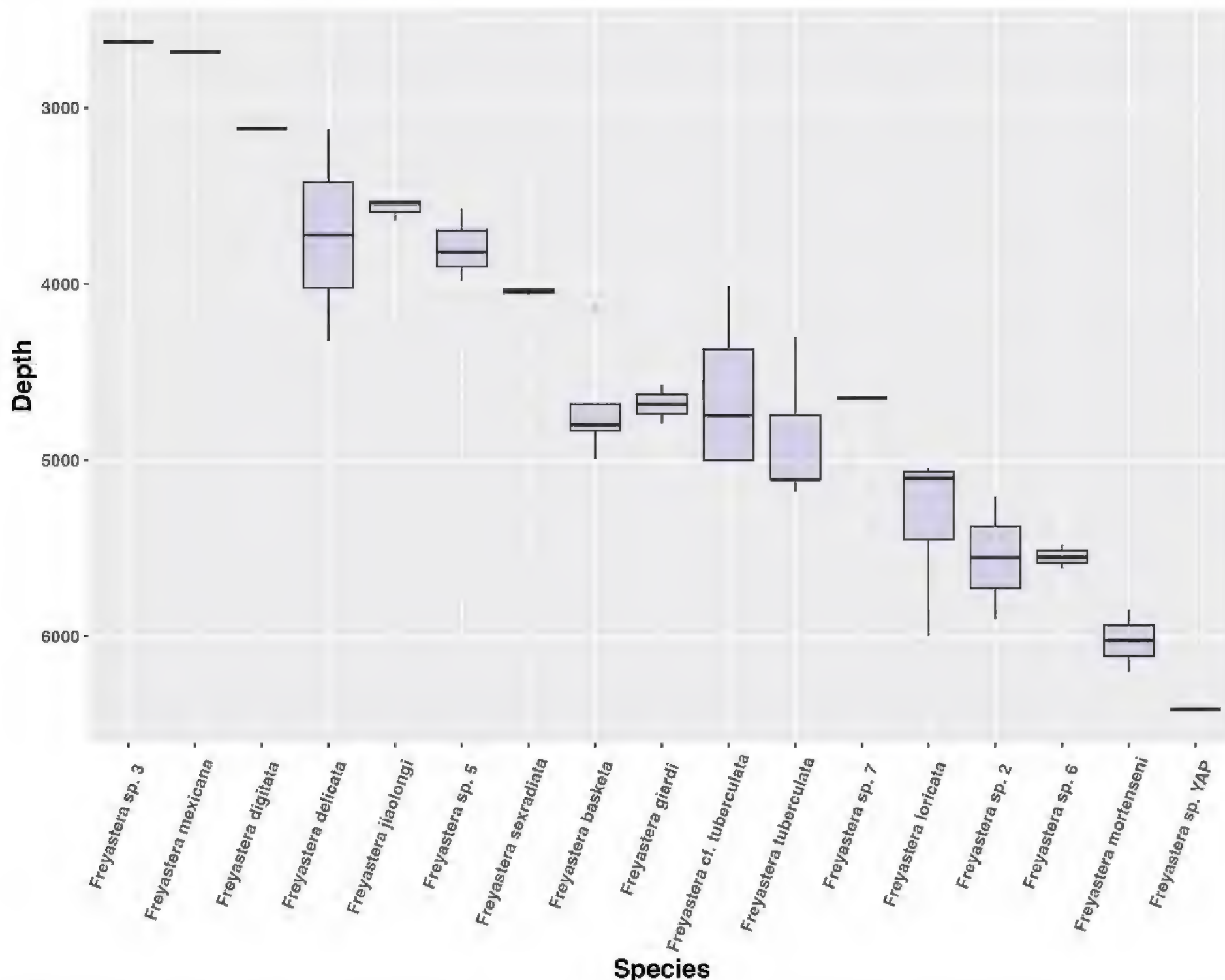


Figure 13. Bathymetric distribution of *Freyastera* species. Data include type localities and specimens examined in the present study.

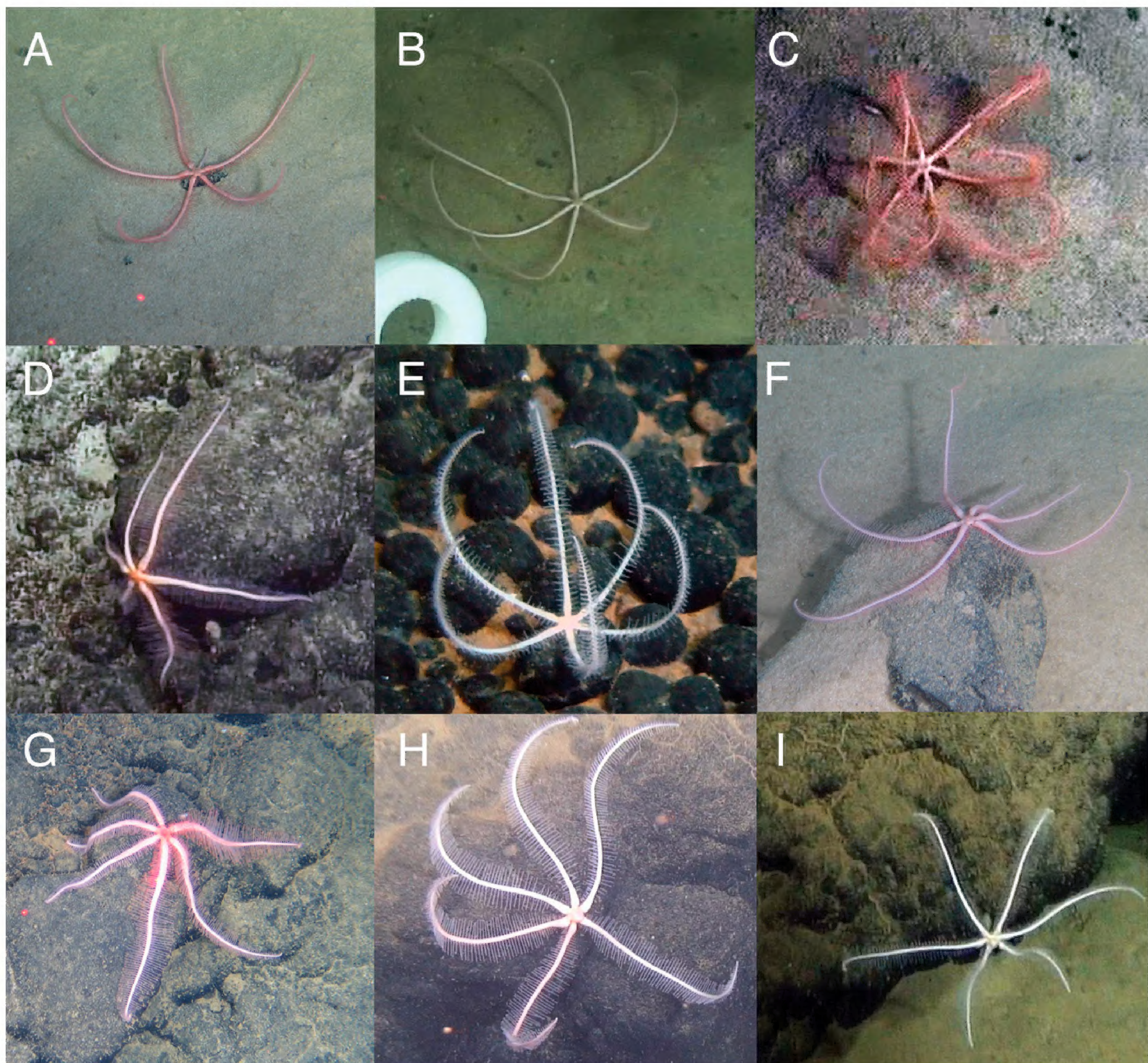


Figure 14. *In situ* photos of *Freyastera* species. **A.** *Freyastera jiaolongi* sp. nov. holotype RSIOAST0117; **B.** *Freyastera jiaolongi* sp. nov. paratype RSIOAST0112; **C.** *Freyastera jiaolongi* sp. nov. paratype RSIOAST0113; **D.** *Freyastera delicata* RSIOAST0135; **E.** *Freyastera basketa* RSIOAST0200; **F.** *Freyastera* sp. 5 RSIOAST0116; **G.** *Freyastera* sp. 5 RSIOAST0107; **H.** *Freyastera* sp. 6 RSIOAST0124; **I.** *Freyastera* sp. 6 RSIOAST0125.

as the same species were also found in non-nodule environments (Zhang et al. 2019). The high diversity of *Freyastera* and its occurrence in various deep-sea environments suggest a successful adaptation and radiation of the genus at great depth.

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Supplementary material 1

List of specimens studied with geographical information and GenBank accession numbers

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Data type: xlsx

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